

2012

Population Size, Habitat Use and Diet of Kittlitz's Murrelets in Prince William Sound, Alaska

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**POPULATION SIZE, HABITAT USE AND DIET OF KITTLITZ'S MURRELETS
IN PRINCE WILLIAM SOUND, ALASKA**

A Thesis Presented

by

ANDREW J. ALLYN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

February 2012

Wildlife and Fisheries Conservation

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ANDREW J. ALLYN

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DEDICATION

I dedicate this work to my family for their ever-lasting support and patience.

ACKNOWLEDGMENTS

This work was conducted with financial support from the Earthwatch Institute and the National Fish and Wildlife Foundation. The U.S. Fish and Wildlife Service Migratory Bird Management Nongame Office Anchorage, Alaska provided logistical support and equipment. I am forever grateful to research technicians Peter Crommett, Nick Nelson and Alex Robbins for their dedicated fieldwork. Numerous Earthwatch volunteers also helped collect data, including Amanda Adley, Samantha Arthur, David Brindle, Mario Rivera, Dan Smith, Rebecca Speer and Julie Stayner. I would also like to thank the graduate student community for their help answering many data analysis questions along the way. Lastly, Beth Pattinson and Karen Brenneman were always gracious enough to provide rides to the airport and housing whenever I needed them in Anchorage.

David Irons and Kathy Kuletz from the U.S. Fish and Wildlife Service Migratory Bird Management Nongame office provided support and thoughtful conversations throughout this study. They were always willing to share their knowledge of seabird ecology. Although I was never formally either David's or Kathy's graduate student, I am thankful that they treated me as such.

I thank my advisor, Curtice Griffin, for his time and guidance throughout this entire process; I am forever indebted to Curt for taking a chance and accepting a student who admittedly probably didn't look like a very promising applicant on paper. I am also thankful for the amazing amount of time and effort Kevin McGarigal dedicated to this study, and for his guidance throughout my master's program. I also want to thank Paul Sievert for all of the insightful conversations over the years, and Mark Leckie for his thoughtful comments on glaciers and oceanographic processes.

Lastly, and most importantly, none of this would have been possible if Aly McKnight and Kelsey Sullivan hadn't agreed to hire an English major, with virtually no wildlife or ecology background, back in May of 2007. Thank you both for giving me a chance, and for your continued guidance, support and friendship. I look forward to many more years of seabird work together, and I hope we can all return to Prince William Sound for some survey work, or maybe just a silver salmon fishing adventure.

ABSTRACT

POPULATION SIZE, HABITAT USE AND DIET OF KITTLITZ'S MURRELETS IN PRINCE WILLIAM SOUND, ALASKA

FEBRUARY 2012

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Directed by: Professor Curtice R. Griffin

During the summer of 2008 and 2009, we studied the ecology of the Kittlitz's Murrelet (*Brachyramphus brevirostris*), a small diving seabird, in Prince William Sound (PWS), Alaska. Population declines in recent decades throughout many core Kittlitz's Murrelet population areas in Alaska, including PWS, have put this species on numerous conservation lists, including the International Union for Conservation of Nature and Natural Resources Critically Endangered List and the United States Endangered Species Candidate List. However, causes of these declines have yet to be determined, and much of the species general ecology remains a mystery, as research efforts are hampered by the birds' occurrence in remote glacial fjords and by their cryptic, solitary nesting behavior that precludes standard breeding site-based monitoring. Here, I update the PWS Kittlitz's Murrelet population estimate, investigate Kittlitz's Murrelet daytime habitat use patterns in PWS, and examine the diet and foraging behavior for a subset of the Kittlitz's Murrelet PWS population.

In Chapter 1, I update PWS population estimates from 2001 and model Kittlitz's Murrelet daytime habitat use using at-sea Kittlitz's Murrelet observation data collected during 2009. Population estimates from comparisons between bootstrapped datasets for 2001 and 2009 with

identical transect compositions suggest that the PWS Kittlitz's Murrelet population significantly increased from 2001 to 2009. The habitat use model indicated that water depth, distance to glacier, distance to shore, and distance to moraine had the greatest influence on Kittlitz's Murrelet daytime habitat use patterns within the study fjords; individuals were observed in shallower waters, closer to glaciers, the shoreline, and further from moraines than the average available habitat.

In Chapter 2, I investigated Kittlitz's Murrelet daytime habitat use patterns in relationship to landscape features and temperature-depth profiles during June and July 2008 in Harriman Fjord and Heather Bay, PWS, Alaska. In Harriman Fjord, Kittlitz's Murrelets were observed in habitats near upwelling areas, indicated by a cold-water wedge near the surface in the temperature-depth profiles. In addition, these locations were also closer to the dominant tidewater glacier, shallower in depth, and further from shore than the average available habitat. In Heather Bay, Kittlitz's Murrelets used locations with a cold, fresh surface layer remaining on top of warmer, more saline water, which were also closer to the glacial moraine, shallower, and closer to shore than the average available habitat.

In Chapter 3, I examined the diet and foraging behavior of Kittlitz's Murrelets in northwestern PWS using stable carbon and nitrogen isotopes and radio telemetry methods from data collected during the summer of 2009. There was no significant difference in either carbon or nitrogen isotope signatures between sexes within the breeding and non-breeding seasons. During the early breeding season, isotope mixing model results suggest individuals foraged on a combination of zooplankton and fish. During the post-breeding season, in contrast, demersal fish and near-surface pelagic fish, possibly from the Bering Sea, dominated Kittlitz's Murrelet diet. Radio-tagged individuals foraged in rapid bouts with short dives and rests, punctuated by longer loafing periods.

Overall, this research updates the population estimate within a core population area for this rare and elusive species, while filling crucial knowledge gaps concerning characteristics of the population's general ecology.

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CHAPTER 1

INTRODUCTION

The Kittlitz's Murrelet, a small diving seabird of the Alcidae family, has a breeding range limited to the waters of Alaska and Eastern Siberia, with 95% of its population located in Alaska (Day et al. 1999). Prince William Sound (PWS), Alaska is one of the core population areas for Kittlitz's Murrelets, accounting for a significant proportion of the Alaska Kittlitz's Murrelet population (USFWS 2010, Kuletz et al. 2011). Estimates of Kittlitz's Murrelets from marine bird surveys throughout PWS suggest that the population declined by 13% per year between 1989 and 2007 (Kuletz et al. 2011). Similar population declines were reported during recent decades in other core Kittlitz's Murrelet population areas throughout Alaska (Arimitsu et al. 2011, Piatt et al. 2011). Largely as a result of these declines, Kittlitz's Murrelets are currently a Candidate for the Endangered Species List (USFWS 2011), designated as "critically endangered" by BirdLife International (2007), and included in the National Audubon Society's Top Ten Endangered Birds List of the United States (National Audubon Society 2006).

Kittlitz's Murrelet low population numbers, patchy distributions within dynamic habitats, and their puzzling nesting habits, limit our ability to answer basic ecological questions concerning this rare seabird species. Therefore, the causes of these widespread population declines remain largely unknown. In this project, we investigated Kittlitz's Murrelet ecology during 2008 and 2009 in PWS, Alaska to (1) assess the current Kittlitz's Murrelet PWS population size, (2) identify variables that characterize Kittlitz's Murrelet habitat use, and (3) examine Kittlitz's Murrelet diet and foraging behavior. Updating estimates for this important core population of Kittlitz's Murrelets in PWS, while expanding our understanding of Kittlitz's Murrelet habitat use

and foraging ecology, are crucial components for developing conservation programs for this species in PWS and other core population areas.

Overall, this thesis includes four chapters, including this general introduction and three subsequent chapters that were written for publication in scientific journals. Although I accept complete responsibility for the contents of this thesis, I use the personal pronoun “we” throughout the thesis because these works represent the collective efforts of many researchers, and to facilitate the conversion of thesis chapters to journal manuscripts

CHAPTER 2

POPULATION SIZE AND HABITATS OF KITTLITZ'S MURRELETS

IN PRINCE WILLIAM SOUND, ALASKA

2.1 Abstract

During the summer 2009, we conducted surveys for Kittlitz's Murrelets (*Brachyramphus brevirostris*) in Prince William Sound, Alaska to update population estimates from 2001 and to model Kittlitz's Murrelet daytime habitat use. We observed a total of 660 Kittlitz's Murrelets; 191 on pelagic transects and 469 on shoreline transects. Our overall population estimate was 2079 birds (95% CI = 1409 – 2990). In comparison, Kuletz et al. (2003) observed a total of 346 Kittlitz's Murrelets in 2001; 134 on pelagic transects and 212 on shoreline transects, resulting in a population estimate of 1400 birds (95% CI = 977 – 1889). This apparent increase in the Kittlitz's Murrelet population was significant using comparisons between bootstrapped datasets for 2001 and 2009 with identical transect compositions. Additionally, we used a paired logistic regression model of presence-only daytime data and spatial data to describe and predict optimal habitat within surveyed fjords and bays. Kittlitz's Murrelets were observed in shallower waters and closer to glaciers, closer to shore, and further from moraines than the average available habitat during daylight hours. Model validation using two independent data sets showed that the model performed quite well; Kittlitz's Murrelets were generally observed at locations where the model predicted high relative likelihood of occurrence values (median predicted relative likelihood of occurrence values range: 0.78 to 0.89). Although Kittlitz's Murrelet numbers appear to have increased since 2001, the low overall population levels and specialized habitat requirements may make Kittlitz's Murrelets especially susceptible to future population threats.

Key Words

Brachyramphus brevirostris, Kittlitz's Murrelet, population size, seabird habitat, at-sea surveys, paired logistic regression, case-controlled logistic regression, presence-only data, habitat model

2.2 Introduction

Kittlitz's Murrelets (*Brachyramphus brevirostris*) are small diving seabirds whose breeding ranges are limited to the waters of Alaska and Eastern Siberia, with 95% of the global population occurring in Alaska (Day et al. 1999). Although the species is listed as a Candidate Species for the Endangered Species List (USFWS 2011), the status of the Kittlitz's Murrelet in Alaska is uncertain with large differences between recent population estimates. The U.S Fish and Wildlife Service estimated the statewide Alaska Kittlitz's Murrelet population at 19578 birds (range: 8190 – 36193) based on surveys between 1999 and 2008 (USFWS 2010). McKnight et al. (2008) reported that the Kittlitz's Murrelet population in Prince William Sound (PWS), which accounts for a significant proportion of the Alaskan population (USFWS 2010), declined 69% from 107354 (\pm 17210) birds in 1989 to 33557 (\pm 8710) birds in 2007.

Despite survey efforts throughout much of Kittlitz's Murrelets Alaskan range, few surveys used the same survey design and protocols. Additionally, in PWS where U.S. Fish and Wildlife (USFWS) marine bird and mammal survey designs and protocols were consistent, the survey was primarily designed to monitor seabird populations following the 1989 Exxon Valdez Oil Spill. Thus, transects excluded several important Kittlitz's Murrelet habitats (McKnight et al. 2008), especially those areas close to the face of tidewater glaciers and glacial outflow regions (Day et al. 2003, Kuletz et al. 2003). The absence of uniform surveys and protocols for Kittlitz's Murrelets prompted some

researchers to suggest that population declines could be an artifact of sampling and data analysis methods (J. Hodges pers. comm., Kirchhoff et al. 2010). Thus, a primary purpose of our study was to determine if the numbers and distribution of Kittlitz's Murrelets have changed in PWS since the 2001 surveys conducted by Kuletz et al. (2003). Further, our survey results provide a more reliable assessment of the Kittlitz's Murrelet population status in PWS, as opposed to the broader USFWS marine bird and mammal surveys. Additionally, we report on Kittlitz's Murrelet daytime habitat use in relation to bathymetry and landscape features to help identify possible conservation and management areas.

2.3 Methods

2.3.1 Study Area

PWS is a large, glaciated embayment located in south-central Alaska that includes 5000 km² of shoreline (marine habitat within 200 m of land) and approximately 9000 km² of water surface area. PWS is surrounded by the Chugach National Forest, which contains 21320 km² of glaciers and ice fields (Molnia 2007). The terminuses of approximately 20 tidewater glaciers occur within PWS (Molnia 2001), providing abundant freshwater inputs, as well as glacial outflow of freshwater, silt and ice, particularly during summer months. PWS waters have a diurnal tidal cycle, and the weather is characterized by frequent cloud cover and precipitation (Wilson and Overland 1986).

Depth within the glacial fjords varies from >400 m to less than five meters above shallow shoals and sills. Bays without tidewater glaciers have much less depth variation

with depths typically <50 m. Fjords with tidewater glaciers generally have stronger temperature and salinity gradients, and cooler and less saline waters than fjords without tidewater glaciers (Gay and Vaughan 1998).

2.3.2 Population Abundance and Distribution

2.3.2.1 Data Collection

During summer 2009, we repeated the surveys of 17 fjords in PWS, originally surveyed in 2001 by Kuletz et al. (2003, 2011) (Fig. 2.1). Within each fjord, two observers surveyed the entire shoreline (marine habitat within 200 m of land) as well as cross-fjord pelagic transects (100 m in front and to both sides of the vessel), from a 7 m vessel traveling at 10-15 km/h. Although there are historic observations of Kittlitz's Murrelets in the southeastern and central parts of PWS, no Kittlitz's Murrelets were observed in these areas of PWS during recent (2007) USFWS marine bird and marine mammal surveys. Thus, these areas of PWS were excluded from our surveys in 2009.

Our 2009 surveys were conducted between 29 June and 31 July to coincide with the chick-rearing phase (Day et al. 1999), when estimates of Kittlitz's Murrelets at-sea are usually highest (Kuletz and Kendall 1998, Speckman et al. 2004, Stephensen 2009). During the 2001 surveys, four fjords were surveyed multiple times throughout the summer (Kuletz et al. 2003). For comparison, we selected surveys conducted between 1 June and 29 July 2001 based on the best temporal overlap with our 2009 surveys. Therefore, the 2001 data used for comparison did not always coincide with the maximum number of Kittlitz's Murrelets observed on each transect during the 2001 surveys. Further, because of different ice and tide conditions, there was variation in transect

lengths and areas between the two survey years. Thus, we calculated each pelagic survey area (Table 2.1) separately using the boat tracks from each year.

Within each fjord, we stratified the survey area to differentiate between pelagic waters (>200 m from shore) and shoreline waters (<200 m from shore). We recorded species (Kittlitz's, Marbled Murrelet (*Brachyramphus marmoratus*), or unidentified Murrelet) and number of birds onto a laptop computer running Program dLOG (Glenn Ford Consulting Inc., Portland, OR). Observers recorded all bird species within 100 m of either side of the vessel (200 m wide strip) using 10x binoculars. We assumed 100% detection within the 200 m wide survey strip; observers were thoroughly trained in Murrelet identification and in distance estimation. A connected handheld GPS unit (Garmin GPSMAP-76) stamped each sighting with geographic coordinates and documented the path of the survey vessel. Crews made every effort not to double-count individuals by noting when birds flushed to points further along the transect, although a low rate of double counting could have occurred. We used all observations in our population estimates. Flying birds, however, were not included in our habitat use analysis as we were unable to meaningfully associate them with a single location.

At-sea survey data from four independent sources were used to evaluate the performance of our Kittlitz's Murrelet habitat use model. One of these data sets included the identical transects we surveyed in 2009, and was collected in 2001 by Kuletz et al. (2003). We also used the three most recent U.S. Fish and Wildlife Service (USFWS) summer PWS marine bird and mammal surveys conducted in 2005, 2007, and 2010 (McKnight et al. 2006, 2008, D. B. Irons, unpubl. data). The USFWS PWS survey was primarily designed to monitor seabird populations following the 1989 Exxon Valdez Oil

Spill. Thus, transects excluded several important Kittlitz's Murrelet habitats (McKnight et al. 2008), especially those areas close to the face of tidewater glaciers and glacial outflow regions (Day et al. 2003, Kuletz et al. 2003). All surveys used identical survey protocols as those used in our 2009 survey.

2.3.2.2 Data Analyses

We calculated population estimates for both 2001 and 2009 using a ratio estimation technique (Strong et al. 1995, Stehman and Salzer 2000). To obtain a pelagic density estimate for each surveyed fjord, we divided the total pelagic count by the total pelagic area surveyed within a fjord. We then extrapolated the pelagic density to the total pelagic area available within the fjord. Because we surveyed the entire shoreline of each fjord, we treated the count from shoreline transects as a census rather than an estimate. Finally, we added each fjord's pelagic population estimate to the shoreline counts for that fjord, and summed across all fjords to obtain the PWS population estimate.

We calculated confidence intervals of point estimates for each survey using a custom non-parametric bootstrap technique (Efron and Gong 1983) created in Program R (R Development Core Team 2010) to resample the pelagic counts and areas within a fjord with replacement ($N = 10000$). For each iteration, we used the population estimation technique outlined above, and then calculated the 0.025 and 0.975 quantiles of the resulting distribution.

We modified the bootstrap to resample the 2001 and 2009 data with replacement to test for a significant difference in Kittlitz's Murrelet population estimates between years. Instead of resampling the original datasets for each year independently, we

sampled the same transects for both years within a single bootstrap iteration. Therefore, for a single bootstrap iteration, the sample of transects contributing to each dataset were identical. After creating a new dataset for each year, we calculated the PWS population estimate using the calculations outlined above. We then subtracted each 2009 estimate from the corresponding 2001 estimate. We determined that the years were not significantly different if 95% of the distribution (i.e., values between the 2.5% and 97.5% quantiles) of the differences between 2009 and 2001 estimates included zero.

2.3.3 Habitat Use

2.3.3.1 Data Collection

To investigate Kittlitz's Murrelet habitat use, we distinguished between "used" and "available" habitat. We defined "used habitat" based on the longitude and latitude location assigned to each Kittlitz's Murrelet observation. In the analysis described below, our response was restricted to presence-only locations; absences were not explicitly recorded during surveys or considered in the analysis. We considered treating the entire transect as the unit of observation or subdividing the transect into arbitrary segments of fixed length and treating the count or density of Murrelets as the response variable, but this required aggregating the data to a coarse and arbitrary scale with unknown implications. We concluded that analyzing the data as presence-only data best represented both the spatial resolution of the raw data (i.e., point locations) and the survey design, and had the added advantage of not requiring an arbitrary aggregation or rescaling of the data. We defined "available habitat" as the entire fjord area, including the used habitat. We sampled the available habitat by creating a 100 x 100 m grid over each

fjord using ArcGIS v. 9.3 (ESRI 2008); we then extracted the latitude and longitude centroid for each grid cell and used these locations as our representative available habitat points.

We used Program R (R Core Development Team 2010) to calculate five spatial landscape (habitat) variables at each used and available location: 1) water depth, and shortest distance to 2) shoreline, 3) glacier, 4) moraine, and 5) freshwater streams/outflow. We created a water depth raster layer from a PWS bathymetry ASCII file (resolution: 200 m) (Kiefer et al. 2008). Using this bathymetry file in combination with NOAA charts, we identified submerged moraines as shallow (0-30 m) arms extending into and/or across fjords/bays. Satellite images (U.S. Geological Survey Global Visualization Viewer Landsat Archive) from July 2009 provided the terminus position of each tidewater glacier during the survey year. We defined the shoreline and locations of freshwater streams using a data layer provided by the U.S. Forest Service (USDA Forest Service 2008a, USDA Forest Service 2008b). We assigned depth values for each used and available point from the bathymetry raster file (Kiefer et al. 2008) using the inverse distance weighting function in the gstat package (Pebesma 2004). We used the shortestPath function in the gdistance package (van Etten 2011) for all over-water distance calculations. We restricted distances to the over-water distance between a point and landscape feature (glacier, moraine and outflow) by setting the land conductance value to 0 and the ocean conductance value to 1.

Finally, we paired the habitat measures for each used point with the average values for available points within the same fjord. To do this, we first averaged all the values for each variable over all the available locations in each fjord. We then subtracted

each average value from the corresponding value for each used point. This process generated a file containing a line for every used location that included fields for differences between used and available for each of the five habitat variables.

2.3.3.2 Data Analyses

We modeled the difference in daytime habitat use and availability for the five landscape variables using a generalized linear model (GLM) with a binomial error distribution, logit link function, and no intercept (Breslow and Day 1980). Our full model prior to accounting for spatial autocorrelation was then of the form:

$$\text{Logit}(p) = B_1 * \text{depth} + B_2 * \text{dist.shore} + B_3 * \text{dist.glacier} + B_4 * \text{dist.moraine} + B_5 * \text{dist.stream} - 1 \quad (2.1)$$

Because of the patchy distribution of Kittlitz's Murrelets in PWS, we assumed the GLM residuals would be spatially autocorrelated. However, there is not a formal, well-established test for spatial autocorrelation for GLM residuals (R. Bivand, pers. comm.). Therefore, following the procedures of Dormann et al. (2007), we attempted to remove spatial autocorrelation by calculating eigenvectors from a defined connectivity matrix. We represented the spatial autocorrelation among Kittlitz's Murrelet observations as a continuous gradient from zero to one by weighting paired observations within a fjord as a function of the maximum distance between bird observations in the fjord. We added a decision rule that accounted for observations from different fjords (a and b) to the

function outlined by Dormann et al. (2007) and calculated the weight between observation i and j as follows:

$$[W_{ij}] = \begin{cases} 0 & \text{if } i \neq j \\ 0 & \text{if } d_{ij} > t \\ \left[1 - \left(\frac{d_{ij}}{t} \right)^2 \right] & \text{if } d_{ij} \leq t \end{cases} \quad (2.2)$$

where d_{ij} was equal to the Euclidean distance (m) between two bird observations (i and j), and t was equal to the maximum distance between two bird observations in one fjord. Although this maximum distance is large within larger fjords, it allowed us to represent the spatial autocorrelation within a fjord as a gradient from zero to one, instead of interpreting the spatial autocorrelation as a binary response when d_{ij} was greater than t .

We used the Moran Eigenvector filtering (ME) function in the spdep package (Bivand 2010) to calculate eigenvectors for the centered weight matrix. Eigenvectors were then added as individual variables to the full model, in order of ascending Moran's I statistic, sequentially until the spatial autocorrelation in the resulting residuals was non-significant ($\alpha \leq 0.05$).

We analyzed all subsets of the full model, but forced the significant spatial eigenvectors derived from the residuals of the full model into all subsets. We evaluated model significance using a likelihood ratio test in the lmer R package (Zeileis and Hothorn 2002), and evaluated competing models using AICc.

We validated our best model based on AICc by examining the predicted relative likelihood of Kittlitz's Murrelet occurrence at observed Kittlitz's Murrelet locations in

our 2009 survey data set (i.e., the same data used to build the model), and in our two independent data sets, including the 2001 survey and the USFWS marine bird and mammal surveys conducted in 2005, 2007 and 2010 combined. First, we used the parameter estimates from the best model to predict the relative likelihood of Kittlitz's Murrelet occurrence at all available habitat locations (i.e., the 100 x 100 m grid of points used to measure available habitat). We then created a surface of the predicted relative likelihood of occurrence (PRLO) for Kittlitz's Murrelet using the Gaussian Kriging function in ArcGIS (ESRI 2008). Next, we overlaid Kittlitz's Murrelet observations from the modeled data, as well as Kittlitz's Murrelet observations from the independent data sets, on the PRLO surface. Finally, we extracted the PRLO value at each Kittlitz's Murrelet observation location, plotted the kernel density distribution of PRLO values at these locations and calculated the median PRLO value across observed Kittlitz's Murrelet locations for each of the three data sets.

2.4 Results

2.4.1 Population Abundance

In 2009, we observed a total of 660 Kittlitz's Murrelets; 191 on pelagic transects and 469 on shoreline transects (Table 2.2, Fig. 2.2). The 2009 Kittlitz's Murrelet population estimate was 2079 birds (95% CI = 1409 – 2990). Kuletz et al. (2001) observed a total of 346 Kittlitz's Murrelets; 134 on pelagic transects and 212 on shoreline transects (Table 2.2, Fig. 2.2). The Kittlitz's Murrelet population estimate for 2001 was 1400 birds (95% CI = 977 – 1889). The 2009 Kittlitz's Murrelet population estimate was significantly greater than the 2001 Kittlitz's Murrelet population estimate when

comparisons were made between bootstrapped datasets for 2001 and 2009 with identical transect compositions (Fig. 2.3).

2.4.2 Distribution

The 2009 daytime distribution of Kittlitz's Murrelets in PWS was similar to the distribution documented in 2001 (Kuletz et al. 2003, 2011) using the same transects, with the exception of Columbia Bay, where we found a much higher density of Kittlitz's Murrelets in 2009. During 2001 surveys, Kuletz et al. (2003) observed Kittlitz's Murrelets in 9 out of the 17 surveyed fjords. In 2009, Kittlitz's Murrelets were observed in 11 of the 17 surveyed fjords. Among the occupied fjords, College Fjord and Harriman Fjord had the highest Kittlitz's Murrelet population estimates in both years (Kuletz et al. 2011).

2.4.3 Habitat Use

The spatial autocorrelation in the full model was removed by two eigenvectors. The resulting global model, with the spatial eigenvector variables, explained 88 percent of the variance in the presence data, and was better than both the null model ($p \leq 0.0001$, $df = 7$) and the full model without the spatial eigenvectors ($p \leq 0.0001$, $df = 2$).

Our best model, as measured by AICc, indicated that water depth, distance to shore, distance to glacier, distance to moraine and the two spatial eigenvectors best explained Kittlitz's Murrelet daytime habitat use (Table 2.3), and all of the retained variables in this model were highly significant (Table 2.4). Kittlitz's Murrelets were

observed in slightly shallower waters, closer to shore, closer to glaciers and further from moraines than the average available habitat.

2.4.3.1 Model validation

Kittlitz's Murrelet observation locations for all three surveys generally overlapped with locations of high PRLO values (Figs. 2.4-2.7). Indeed, the median PRLO value at observed Kittlitz's Murrelet locations from our 2009 survey was 0.89, and it was 0.79 and 0.78 from the two independent surveys (Fig. 2.8). However, there were a few areas where observations and corresponding PRLO values did not match well. In Wells Bay and Port Bainbridge, no Kittlitz's Murrelets were observed during the three surveys, yet PRLO values from the model predictions were very high in some locations ($\sim > 0.8$) (Fig. 2.5, 2.6). In contrast, PRLO values were very low in parts of upper Unakwik Inlet, upper College Fjord and Harriman Fjord ($\sim < 0.3$) where we observed considerable numbers of Kittlitz's Murrelets (Figs. 2.6a, 2.6b).

2.5 Discussion

2.5.1 Population Abundance and Distribution

The 2009 PWS Kittlitz's Murrelet population estimate was significantly greater than the Kittlitz's Murrelet population calculated using the 2001 surveys conducted by Kuletz et al. (2003, 2011). Despite this apparent increase, only one juvenile Kittlitz's Murrelet was recorded on USFWS marine bird and marine mammal surveys since 2004 (McKnight et al. 2008), suggesting extremely low Kittlitz's Murrelet productivity in PWS. Further, no juvenile Kittlitz's Murrelets were observed during our survey in 2009. Thus, if there is little recruitment, the PWS Kittlitz's Murrelet population may be very

vulnerable to future population declines despite this apparent increase in abundance since the 2001 survey.

With the exception of Columbia Bay, where Kittlitz's Murrelets were absent during the 2001 survey, Kittlitz's Murrelet distributions within PWS were relatively consistent between the two survey years. Harriman and College Fjord contributed more than half of Kittlitz's Murrelet population estimates for both years, accounting for 80% of the PWS population in 2001, and 56% of the PWS population in 2009.

Kuletz et al. (2003) suggested that Kittlitz's Murrelets distributions may be associated with stable or advancing tidewater glaciers in PWS. In contrast, Kissling et al. (2007) observed high Kittlitz's Murrelet densities near retreating and wasting tidewater glaciers in Icy Bay. In 2009, our highest counts occurred in Columbia Bay, which is influenced by Columbia Glacier, the fastest retreating previously classified tidewater glacier in PWS. Further, the glacier's terminus is over 12 km from the head of the bay. Despite this large distance to the terminus of the glacier, the glacier still heavily influences the waters of Columbia Bay when outgoing tides regularly transport ice over a moraine into the bay. This influx of ice into the bay may simulate upwelling processes; we regularly observed Kittlitz's Murrelets and other seabird species (primarily Black-Legged Kittiwakes [*Rissa tridactyla*]) foraging extensively along the moraine in 2009. Foraging birds also seemed to be in close proximity to highly turbid waters extending from the moraine into the bay. Interestingly, no Marbled Murrelets were seen in this area in 2009. These observations seem to support previous studies that suggest Kittlitz's Murrelets tend to use more turbid waters than Marbled Murrelets (Day et al. 2003, Stephenson 2009).

2.5.2 Habitat Use Within Fjords and Bays

We proposed and tested a cost-effective technique for identifying Kittlitz's Murrelet daytime habitat in PWS using presence-only at-sea survey data and spatial GIS data. Our analysis of Kittlitz's Murrelet habitat use supports previous research in PWS, suggesting that within glacial fjords, Kittlitz's Murrelets use habitats closer to shore and closer to glaciers (Day et al. 2003, Stephensen 2009). Although, Day et al. (2003) observed Kittlitz's Murrelets in deeper waters than the available habitat, and Stephensen (2009) observed Kittlitz's Murrelets closer to moraines and sills, our results indicate Kittlitz's Murrelets used shallower waters further from moraines. These contradictions are likely the result of different study designs. Day et al. (2003) restricted their analysis to waters ≤ 200 m from shore within four fjords. Additionally, Stephensen (2009) examined Kittlitz's Murrelet habitat use within one fjord, while we considered Kittlitz's Murrelet observations and available locations within the entire fjord habitat and across 17 different fjords.

Overall, PRLO values were high at locations where Kittlitz's Murrelets were observed. However, performance did vary depending on the data set used for model validation. Not surprisingly, median PRLO values were highest for the 2009 survey data used to create the habitat use model. The difference in median PRLO values from 2009 survey data to 2001 may indicate small changes in distributions between 2001 and 2009. Additionally, the differences between intensive surveys and the broader USFWS marine bird and mammal surveys median PRLO values is likely the result of the different transects surveyed between intensive fjord and USFWS marine bird and mammal surveys. USFWS marine bird and mammal surveys do not cover several important Kittlitz's Murrelet areas (e.g., southwestern Icy Bay and northeastern College Fjord), consequently, a greater proportion of Kittlitz's Murrelets recorded during USFWS surveys occurred in suboptimal habitat. Despite this shortfall, however, the median

PRLO value for Kittlitz's Murrelet observation locations from the USFWS surveys was still reasonably high (0.78), and close to the median PRLO value from 2001 intensive surveys (0.79) and 2009 intensive surveys (0.89). Further, our model performed well for both "typical" distributions and for distributions occurring during two episodes of abnormally dense aggregations, one in Heather Bay during the summer of 2007 (Allyn et al. 2008) and one in Columbia Bay during the summer of 2009. Although these phenomena had not been previously documented in either bay, in both cases the aggregations occurred in areas with the highest PRLO values.

In a few regions, model predictions did not match well with Kittlitz's Murrelet observations. It appears that in bays without glaciers or moraines, these disparities may be the result of the modeling framework (e.g., areas in Wells Bay, and other bays without glaciers or moraines). One limitation of our use versus availability comparison at the fjord-scale, was we could not include the presence/absence of glaciers or moraines as a factor in the model as there was no difference in use versus availability with respect to these features within a given fjord (i.e., for a given fjord "A" there either is a glacier/moraine or there is not, and there is no difference in this factor at this scale). Subsequently, distance to glacier (or moraine) was calculated to the nearest glacier in a neighboring fjord; areas near the mouth of the target fjord were closer to a glacier than the average available habitat, even though effects from neighboring glaciers were likely negligible because of the general outward water flow from glacial fjord systems.

In fjords with glaciers and moraines, there were a few regions where PRLO values were high and we did not observe Kittlitz's Murrelets (e.g., Port Bainbridge), as well as a few regions where PRLO values were low and we observed relatively high numbers of Kittlitz's Murrelets (e.g. upper Unakwik Inlet, upper College Fjord and Harriman Fjord). These mismatches suggest that factors outside the modeled habitat variables are affecting the habitat quality in these areas.

Port Bainbridge is unique among the modeled fjords in its degree of exposure; it opens directly into the Gulf of Alaska, and it is therefore subject to oceanographic influences very different from the mainland/northern fjords in PWS. Interestingly, however, earlier USFWS surveys (e.g. 1993, 2004) did record a few Kittlitz's Murrelets in Port Bainbridge, all within high PRLO regions (Kuletz et al. 2011). The disagreement between model predictions and survey observations for upper Unakwik Inlet, upper College Fjord, and regions within Harriman Fjord, may be related to factors associated with the advancing status of these tidewater glaciers, and perhaps even the stable status of Harriman Glacier (Molnia 2007), in contrast to the retreating status of all other PWS glaciers. Glacier status (e.g., stable, advancing, retreating), and glacier characteristics (e.g., depth at terminus, size) can have profound influences on calving rates, sedimentation levels and freshwater influx within the fjord system (Post 1975, Koppes and Hallet 2002). These processes, in turn, can affect the physical characteristics of the water column, altering the distribution and composition of biological communities (Dierssen et al. 2002, Etherington et al. 2007). Therefore, these advancing and stable tidewater glaciers may be influencing the physical or biological structure within the fjords through mechanisms not captured by the habitat variables used in our model, allowing Kittlitz's Murrelets to exploit these habitats even though the model predicts relatively low PRLO values (e.g., Arimitsu 2009). Alternatively, these disparities may simply reflect the overall low numbers of Kittlitz's Murrelets in PWS and the consequent inability of birds to utilize all available habitats with high PRLO values.

An important consideration regarding our presence-only modeling framework, and specifically its application to other geographic areas or species, is how we defined available habitat. In the paired logistic regression framework, we used the differences between values at Kittlitz's Murrelet observation locations and values representing the average available habitat. Consequently, model selection, estimated parameters and eventual conclusions are all highly sensitive to how available habitat is defined. For our study, individual glacial fjords represented

meaningful spatial and ecological units to delineate available habitat because PWS Kittlitz's Murrelets in PWS are rarely observed outside fjords during the daytime. However, any application of this modeling framework for Kittlitz's Murrelets or other species would require careful consideration of how to delineate the available habitat.

Conservation efforts for rare, elusive species with home ranges in remote locations, such as the Kittlitz's Murrelet, present numerous logistic and economic challenges. For Kittlitz's Murrelets, these challenges are intensified by the overlap between Kittlitz's Murrelet habitat and human use areas, especially in such popular tourist destinations such as glacial fjords in PWS, Glacier Bay and Kenai Fjords, Alaska. In PWS, over 98% of Kittlitz's Murrelets observations were within such fjords. Certainly, within these systems the habitat use patterns of Kittlitz's Murrelets are influenced by complicated mechanisms, including oceanographic characteristics and the distribution of prey (Arimitsu 2009). However, we suggest that our approach can be applied while we develop a clearer understanding of these dynamics. For example, imposing vessel speed limits and/or no-fish zones in just the areas of occupied glacial fjords having the highest PRLO values could be one strategy for conserving Kittlitz's Murrelets in PWS with minimal effects on commercial and recreational activities.

2.6 Acknowledgements

The National Fish and Wildlife Foundation provided funding for this research; the U.S. Fish and Wildlife Service Migratory Bird Management Program-Anchorage, AK provided logistical support, at-sea survey vessels and equipment. We thank Peter Crommett for his dedicated fieldwork during the summer of 2009.

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Table 2.1. Area of pelagic waters (>200 m from shore) surveyed along 100 m-wide transects and total pelagic area, excluding shoreline (<200 m of shore), by fjord/bay used for extrapolating Kittlitz's Murrelet population estimates for Prince William Sound, Alaska, 2001 and 2009.

Fjord/Bay	Pelagic Area Surveyed (km ²)		Total Pelagic Fjord Area (km ²)	
	2001	2009	2001	2009
Harriman Fjord	6.74	6.28	55.90	53.04
College Fjord	8.95	8.87	88.40	82.19
Icy Bay	4.41	4.78	36.32	38.84
Blackstone Bay	3.08	3.34	35.02	34.67
Heather Bay	0.85	0.78	7.84	6.54
Port Nellie Juan	8.89	9.07	79.56	88.01
Columbia Bay	4.01	3.12	21.62	22.16
Long Bay	2.55	2.72	15.28	14.91
Wells Bay	2.10	2.10	23.22	23.43
Unakwik Inlet	7.52	7.38	72.12	66.71
Eaglek Bay	4.11	3.40	30.98	28.53
Port Wells	12.61	13.03	182.27	179.14
Passage Canal	2.66	2.51	24.65	23.59
Cochrane Bay	2.54	2.34	22.62	22.56
Whale Bay	2.48	2.73	17.85	18.11
Port Bainbridge	7.92	7.91	70.93	71.62

TOTAL	81.42	80.38	784.57	774.05
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Fjord/Bay	Shoreline		Pelagic		Pelagic Density (birds/km ²)		Pelagic Abundance Estimate		Total Fjord/Bay Pop. Estimate	
	2001	2009	2001	2009	2001	2009	2001	2009	2001	2009
Harriman Fjord	44	23	76	63	11.44	10.03	639	532	683	555
College Fjord	27	120	32	53	3.58	5.97	316	491	343	611
Icy Bay	75	19	17	15	3.75	3.07	136	119	211	138
Blackstone Bay	39	9	7	7	2.24	1.88	78	65	117	74
Unakwik Inlet	19	55	0	6	0	0.81	0	54	19	109
Heather Bay	2	17	1	8	1.21	10.29	10	67	12	84
Port Nellie Juan	2	1	1	0	0.11	0	9	0	11	1
Long Bay	2	0	0	1	0	0.37	0	5	2	5
Passage Canal	2	0	0	0	0	0	0	0	2	0
Cochrane Bay	0	6	0	4	0	1.28	0	29	0	35
Columbia Bay	0	219	0	33	0	10.57	0	234	0	453
Drier Bay	0	0	0	0	0	0	0	0	0	0
Eaglek Bay	0	0	0	0	0	0	0	0	0	0

Port Bainbridge	0	0	0	0	0	0	0	0	0	0
Port Wells	0	0	0	1	0	0.08	0	14	0	14
Wells Bay	0	0	0	0	0	0	0	0	0	0
Whale Bay	0	0	0	0	0	0	0	0	0	0
TOTAL	212	469	134	191			1187	1610	1400	2079

Table 2.2. Kittlitz's Murrelets observed on shoreline and pelagic transects, pelagic densities, pelagic abundance estimates and total population estimates by fjord/bay surveyed in 2001 (Kuletz et al. 2003, 2010) and 2009, Prince William Sound, Alaska.

Table 2.3. The best five generalized linear models, as ranked by AICc, describing Kittlitz's Murrelet habitat use in Prince William Sound, Alaska, 2009.

Model	AICc	Δ AICc	AICc Weight
depth + distance to shore + distance to glacier + distance to moraine + spatial eigenvector 1 + spatial eigenvector 2	124.97	0	0.69
depth + distance to shore + distance to glacier + distance to moraine + distance to stream + spatial eigenvector 1 + spatial eigenvector 2	126.66	1.69	0.29
depth + distance to shore + distance to glacier + distance to stream + spatial eigenvector 1 + spatial eigenvector 2	135.26	10.29	0.004
depth + distance to shore + distance to glacier + spatial eigenvector 1 + spatial eigenvector 2	135.73	10.75	0.003
distance to shore + distance to glacier + distance to moraine + spatial eigenvector 1 + spatial eigenvector 2	140.24	15.27	0.000

Table 2.4. Parameter estimates, standard errors (SE) and probability values (P) of best model describing Kittlitz's Murrelet habitat use in Prince William Sound, Alaska, 2009.

Parameter	Estimate	SE	Z value	P ($> z $)
Depth	0.038	0.010	3.84	0.00012
Distance to shore	-4.19	0.96	-4.35	1.34×10^{-05}
Distance to glacier	-1.03	0.17	-5.92	3.24×10^{-09}
Distance to moraine	0.51	0.16	3.29	0.001
Spatial eigenvector 1	-81.56	16.38	-4.98	6.35×10^{-07}
Spatial eigenvector 2	112.10	24.18	4.64	3.54×10^{-06}

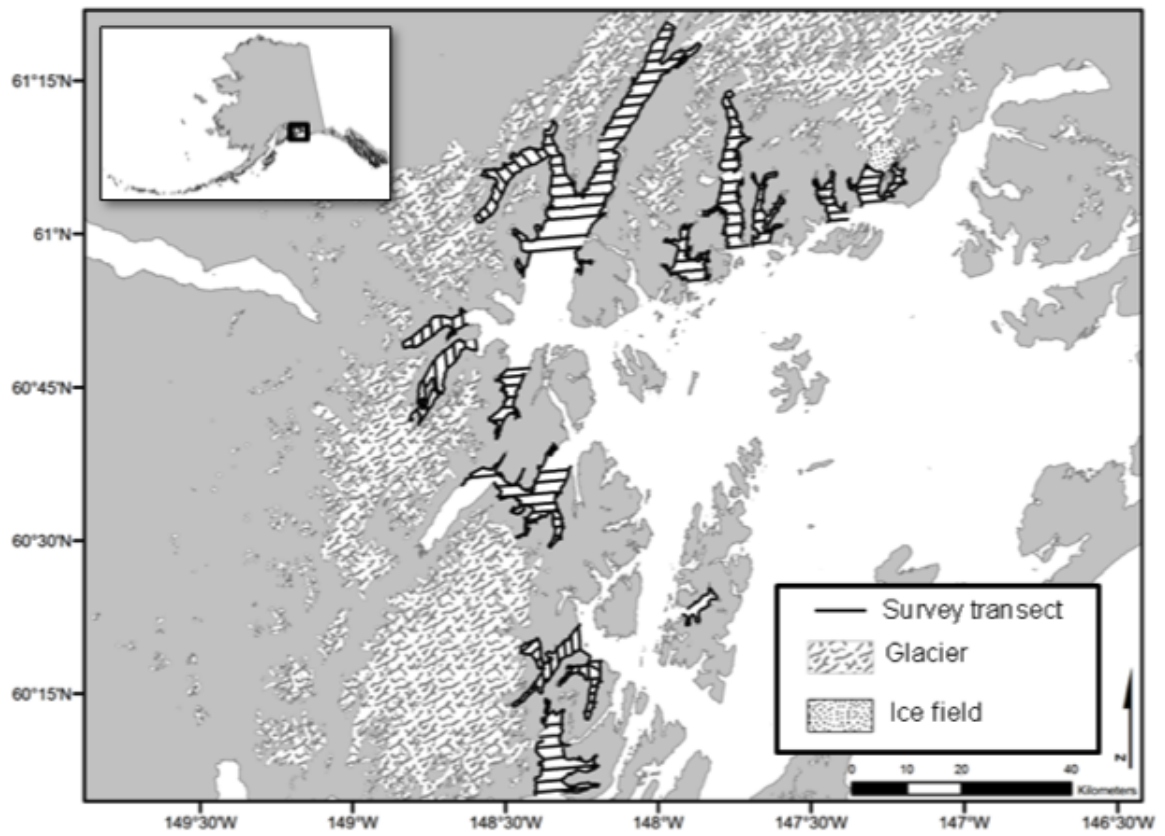


Figure 2.1. Survey transects (black lines) in 17 fjords surveyed in 2001 (Kuletz et al. 2003, 2011) and 2009 Prince William Sound, Alaska.

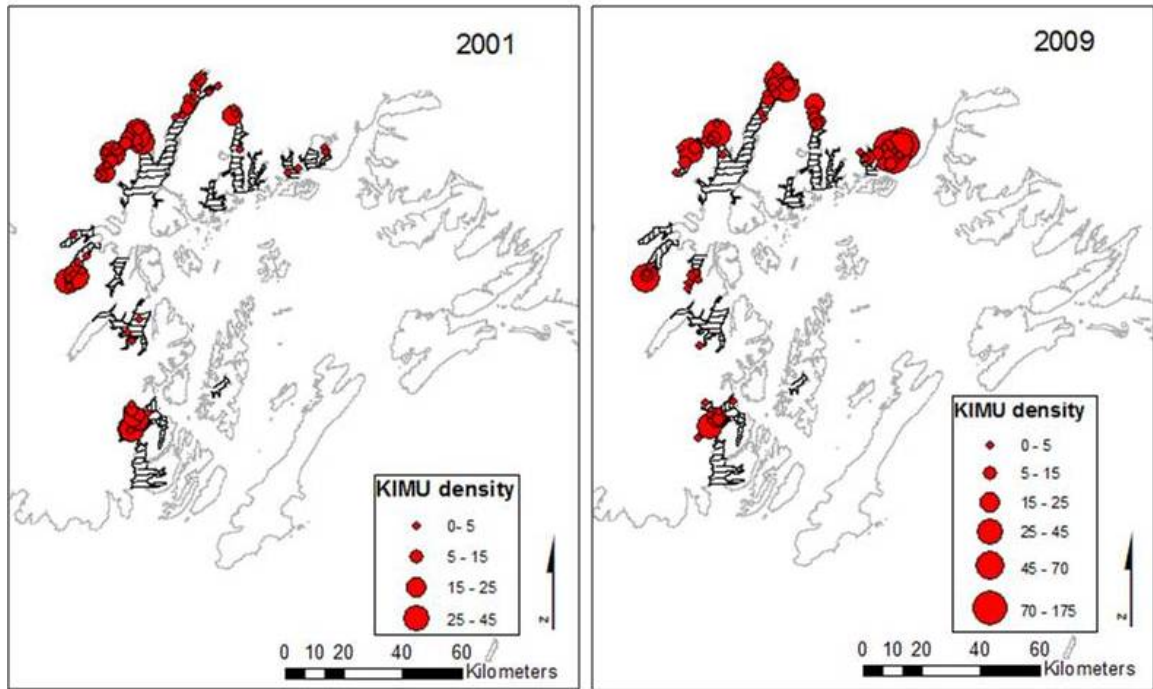


Figure 2.2. Distribution and density (birds/km²) of Kittlitz's Murrelets (KIMU) observed during surveys on transects (black lines) in 17 fjords and bays in Prince William Sound, Alaska in 2001 and 2009 (Kuletz et al. 2003, 2011).

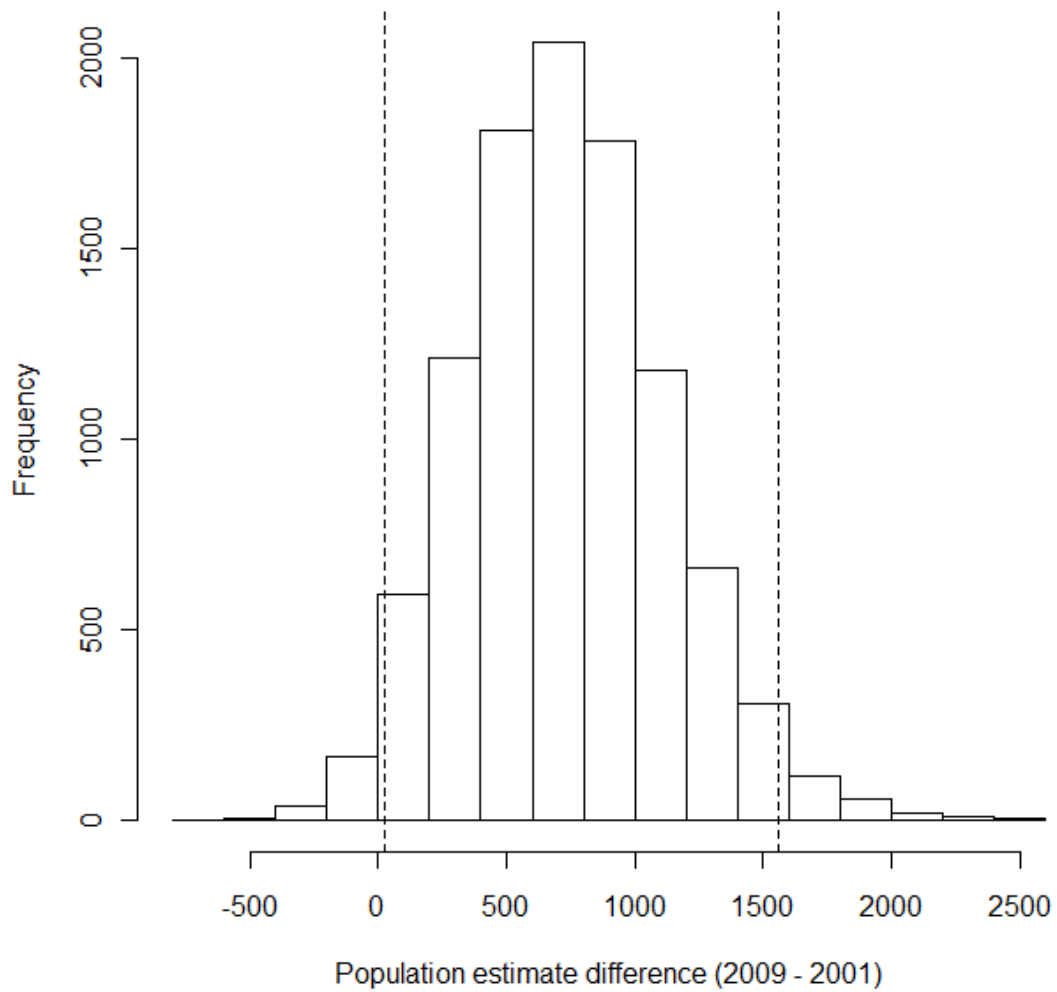


Figure 2.3. Frequency distribution of the bootstrap sample differences between 2009 and 2001 PWS Kittlitz's Murrelet population estimates and 2.5% and 97.5% quantiles (dotted lines).

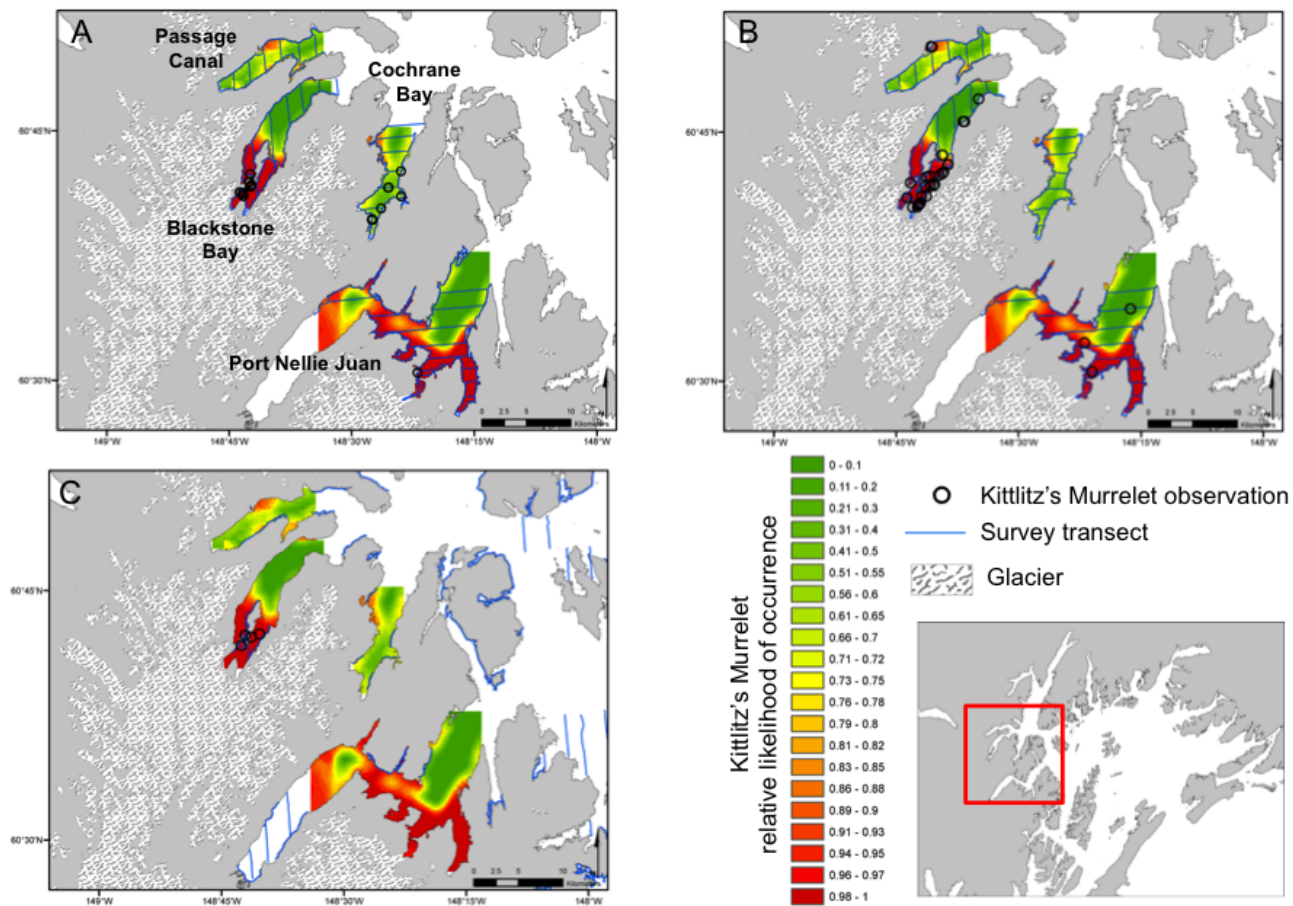


Figure 2.4. Kittlitz's Murrelet observations from 2009 used in model creation (A), independent intensive surveys in 2001 (B), and independent U.S. Fish and Wildlife Service surveys (2005, 2007, 2010) (C) in central PWS, overlaid on Kittlitz's Murrelet relative

likelihood of occurrence prediction surface, which was calculated from the best model describing Kittlitz's Murrelet relative likelihood of occurrence as a function of water depth, distance to shore, and distance to glacier.

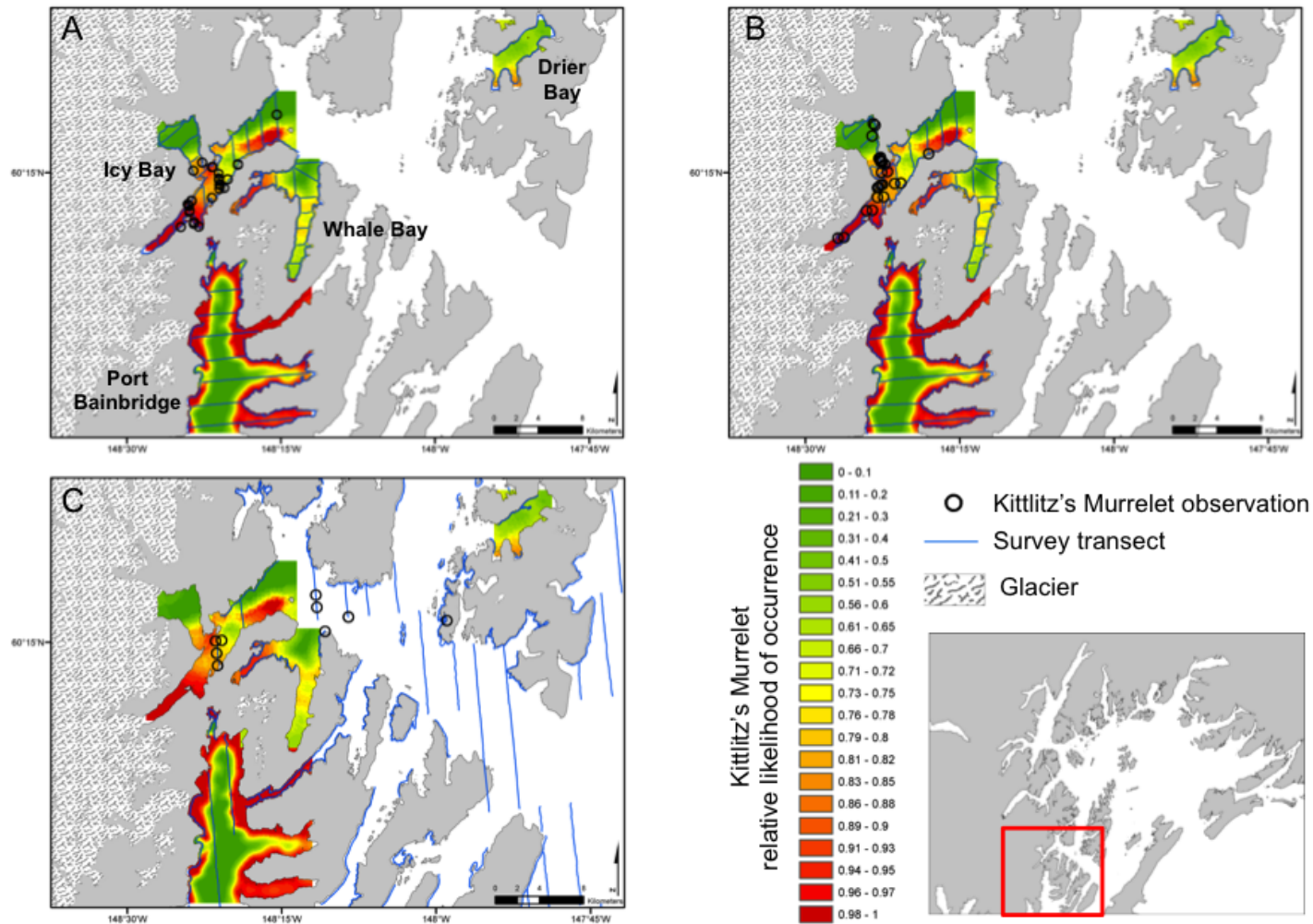


Figure 2.5. Kittlitz's Murrelet observations overlaid on model prediction surface for fjords in southern Prince William Sound Alaska, 2009.

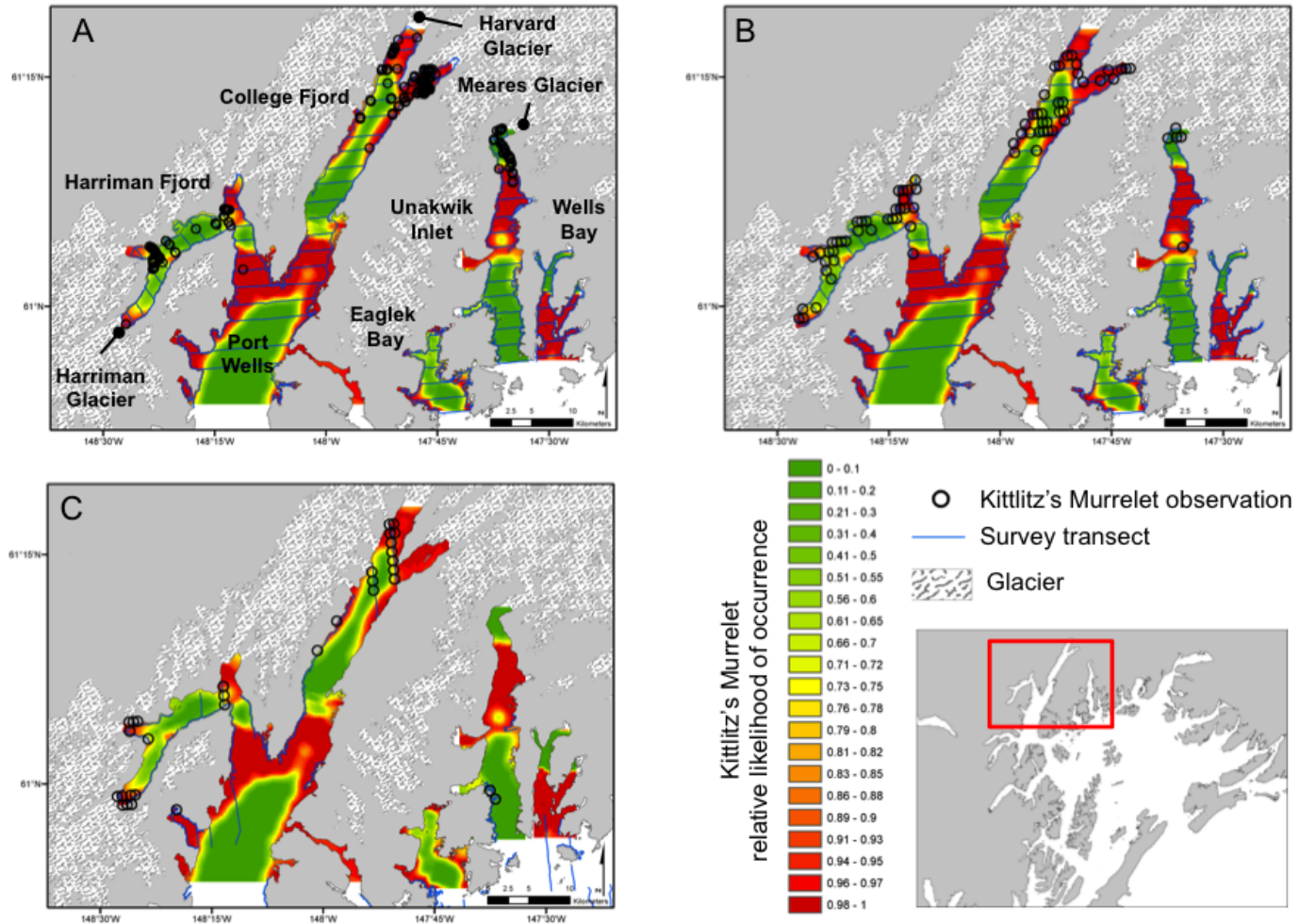


Figure 2.6. Kittlitz's Murrelet observations overlaid on model prediction surface for fjords in northwestern Prince William Sound Alaska, 2009.

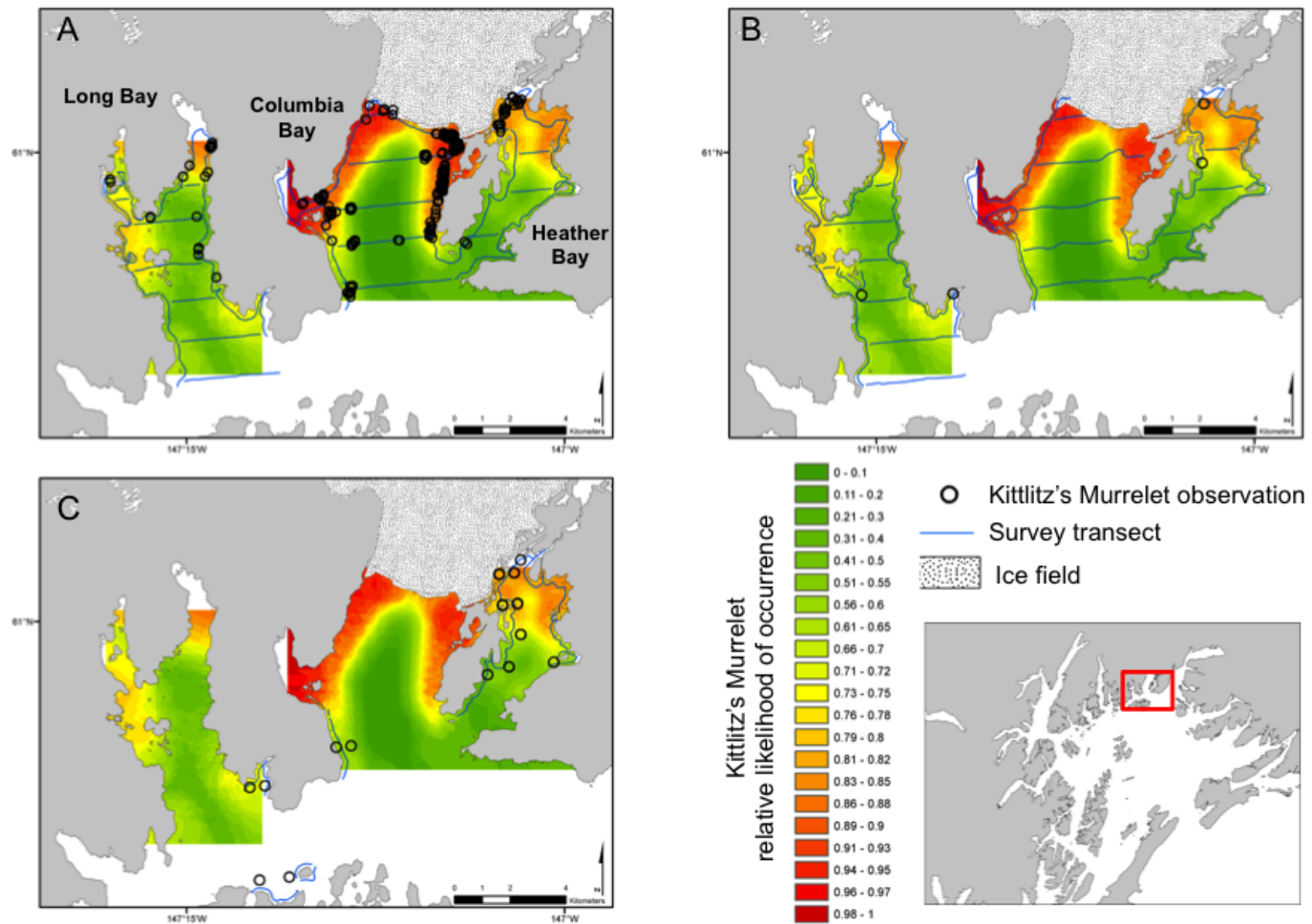


Figure 2.7. Kittlitz's Murrelet observations overlaid on model prediction surface for fjords in northeastern Prince William Sound Alaska, 2009.

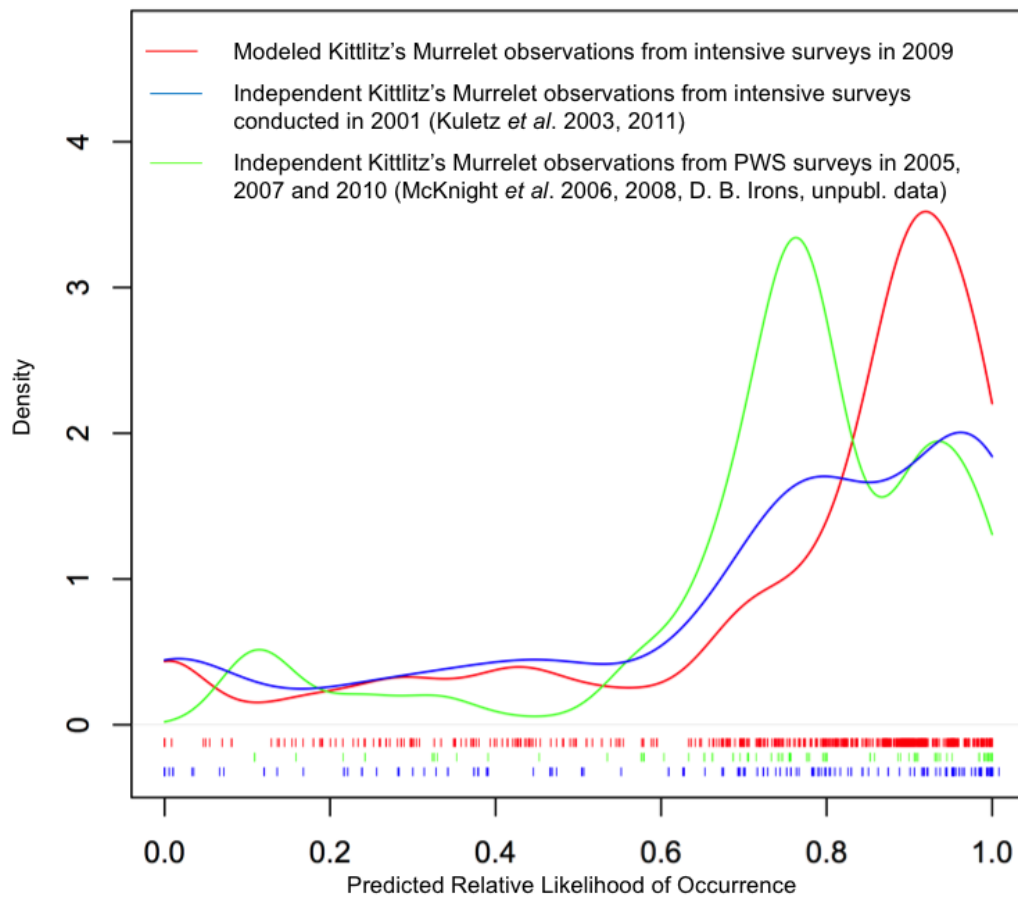


Figure 2.8. Kernel density plots of predicted relative likelihood of occurrence values at observed Kittlitz's Murrelet locations from model-based 2009 survey data (N = 660), independent 2001 survey data of identical transects (N = 346), and independent U.S. Fish and Wildlife Service marine bird and mammal surveys in 2005, 2007, and 2010 (N = 276).

CHAPTER 3

RELATIONSHIPS AMONG KITTLITZ'S MURRELET HABITAT USE, TEMPERATURE-DEPTH PROFILES, AND LANDSCAPE FEATURES IN PRINCE WILLIAM SOUND, ALASKA

3.1 Abstract

Although seabirds search large areas for food, their distributions often correlate with physical characteristics of the marine environment, which can serve to aggregate prey. Kittlitz's Murrelets (*Brachyramphus brevirostris*) are found almost exclusively in Alaskan waters, where they are closely associated with glacial fjords, suggesting that this species might be tightly linked to specific physical habitat characteristics of the fjords. We investigated the relationships among Kittlitz's Murrelet use locations from at-sea surveys, water column characteristics, and landscape features in Harriman Fjord and Heather Bay, Prince William Sound, Alaska. In Harriman Fjord, Kittlitz's Murrelets were observed in habitats near upwelling areas, indicated by a cold-water wedge near the surface in the temperature-depth profiles. In addition, these locations were also closer to the dominant tidewater glacier, shallower in depth, and further from shore than the average available habitat. In Heather Bay, Kittlitz's Murrelets appeared to use locations with a cold, fresh surface layer remaining on top of warmer, more saline water; however, the parameter estimate for this variable was insignificant likely due to limited sample size. Kittlitz's Murrelets in Heather Bay also appeared to use shallower waters closer to shore and closer to the glacial moraine than the average available habitat. Although the best temperature-depth profiles were dramatically different between the two fjords, both of these glacially influenced water column characteristics may serve to concentrate prey at an optimal depth, allowing Kittlitz's Murrelets to focus foraging efforts at predictable locations. Given the widespread wasting of glaciers

throughout their range, Kittlitz's Murrelets may face increased pressure as changes in water column dynamics within glacial fjords affect the distribution and concentration of preferred prey.

Key Words

Brachyramphus brevirostris, Kittlitz's Murrelet, seabird habitat use, conductivity-temperature-depth meter, temperature-depth profile, water column profile, glacial moraines, paired logistic regression, case-controlled logistic regression

3.2 Introduction

The productivity and survival of higher trophic level marine organisms, such as seabirds, are dependent upon their ability to efficiently locate concentrations of prey in a heterogeneous environment. Consequently, seabirds often search large areas for food, but generally congregate where there are high prey concentrations (Durazo 1998). These prey concentrations are often correlated with horizontal and vertical gradients in physical water properties (e.g., temperature, density) (Olson & Backus 1985, Franks 1992, Bakun 1996), boundaries between mixed and stratified waters (Hunt & Schneider 1987), and tidal front areas (Day & Byrd 1989). Bathymetric features (e.g., shallow banks, shoals, slopes and shelves) can also create secondary circulation patterns that aggregate prey (e.g., Hunt et al. 1996, 1998, Allen et al. 2001), and attract seabirds (e.g., Hunt & Schneider 1987, Hunt et al. 1996). These reliable high prey densities in turn increase seabird foraging efficiency and maximize net energy input and could result in better body condition, increasing both survival and productivity rates (e.g., Chastel et al. 1995, Barbraud & Chastel 1999, Daunt et al. 2006).

The Kittlitz's Murrelet (*Brachyramphus brevirostris*), a small diving seabird of the Alcidae family, is found almost exclusively in Alaskan waters (Day et al. 1999)

where they are closely associated with tidewater glaciers and glacial outflow regions (Kissling et al. 2007, Stephensen 2009, Kirchhoff et al. 2010). Within Prince William Sound (PWS), 98% of the Kittlitz's Murrelets are found in glacial fiords during the breeding season with the remaining birds spread sparsely throughout the bays, passes and open areas (Kuletz et al. 2011). With recent widespread population declines of Kittlitz's Murrelets in Alaska (Arimitsu et al. 2011, Kuletz et al. 2011, Piatt et al. 2011) and the uncertainty regarding the effects of climate change on tidewater glaciers, information is needed on the factors that affect Kittlitz's Murrelet distributions in glacial fjord systems. Therefore, in this study, we investigated habitat use of Kittlitz's Murrelets in July 2008 in Harriman Fjord and Heather Bay, two fjords of PWS with exceptionally high densities of Kittlitz's Murrelets, in relationship to temperature-depth profiles and landscape features.

3.3 Methods

3.3.1 Study Area

PWS is a large, glaciated embayment located in south-central Alaska (Fig. 3.1) that includes 5000 km² of shoreline (marine habitat within 200 m of land) and approximately 9000 km² of water surface area. PWS is surrounded by the Chugach National Forest, which contains 21320 km² of glaciers and ice fields with approximately 20 tidewater glaciers that terminate in PWS (Molnia 2001). Abundant freshwater inputs, as well as glacial outflow of freshwater, silt, and ice, have profound effects on this marine ecosystem, particularly during the summer months. During July and August, water temperatures are warmest and surface salinities lowest (Cooney et al. 2001). PWS waters

have a diurnal tidal cycle, and the weather is characterized by frequent cloud cover and precipitation (Wilson and Overland 1986).

Within PWS, we studied Kittlitz's Murrelet habitat use in two glacially influenced locations: Harriman Fjord and Heather Bay (Fig. 3.1). Harriman Fjord ($61^{\circ}02'59''$ N $148^{\circ}22'14''$ W) is approximately 65.6 km^2 in total area (Molnia 2001) and ranges in depth from a few meters to >140 m. Three major glaciers influence the fjord: Serpentine, Surprise and Harriman (Fig. 3.1). Serpentine Glacier has been retreating since the mid-1900s (Lethcoe 1987) and is no longer a tidewater glacier. Surprise Glacier is also retreating but remains a tidewater glacier, as does Harriman Glacier, which is now relatively stable after advancing during the 1990s (Molnia 2007). During intensive Murrelet surveys in 2009, roughly 15% of the Kittlitz's Murrelets observed in PWS occurred in Harriman Fjord (Kuletz et al. 2011). The surrounding landscape of Harriman Fjord contains many high-altitude scree slopes that are believed to be nesting habitat for Kittlitz's Murrelets (Day et al. 1999).

Heather Bay ($60^{\circ}58'30''$ N, $147^{\circ}00'38''$ W) is a 13 km^2 embayment located in the northeastern region of the Sound (Fig. 3.1). Depths in the pelagic region of Heather Bay range from a few meters to 110 m. Adjacent to Heather Bay is Columbia Bay, historical terminus for Columbia Glacier, a large, rapidly retreating tidewater glacier (Molnia 2007) (Fig. 3.1). Although Heather Bay contains no tidewater glaciers, only Heather Island and an exposed glacial moraine separates it from Columbia Bay. The exposed moraine is never completely submerged, but water flows into Heather Bay from Columbia Bay over the moraine at several points during each incoming tide. Columbia Bay has extraordinarily high densities of icebergs at this location because of the damming

effect of the moraine near the entrance to its fjord. Thus, the large tidal influx of water from Columbia Bay into Heather Bay carries ice into Heather Bay. In 2007, during U.S. Fish and Wildlife marine bird and mammal PWS surveys, 75% of the Kittlitz's Murrelets observed in PWS were located in Heather Bay (McKnight et al. 2008). During intensive 2009 Kittlitz's Murrelet surveys, Heather Bay accounted for roughly 5% of the total Kittlitz's Murrelets observed (Kuletz et al. 2011).

3.3.2 Data Collection

3.3.2.1 At-sea surveys

We surveyed Harriman Fjord and Heather Bay three times each during July 2008. We used fjord-specific sampling grids stratified into high and low density Kittlitz's Murrelet areas based on surveys conducted by Stephensen (2009) and Allyn et al. (2008). We surveyed a different subset of available transects during each visit to each fjord (mean = 5 transects/visit, range = 4 – 7 transects) (Table 3.1).

In Harriman Fjord, our sampling grid included six transects, with four and two transects, respectively, in high and low density Kittlitz's Murrelet areas (Fig. 3.2). Transects varied in length from 1000 to 2000 m and were separated by 450 m. Because of the geography of Harriman Fjord, transects ran east-west to align sampling with the dominant physical force in the sampling region: ice and glacial outflow from Surprise Glacier.

In Heather Bay, our survey grid included eight transects with four in high and four in low Kittlitz's Murrelet density areas (Fig. 3.2). High density transect lengths ranged from 200 to 1300 m and were separated by 400 m. Lengths of low density transects ranged from 745 to 2600 m and were separated by 400 m. We surveyed Heather Bay transects in the north-south direction to align

sampling with the dominant physical force in the bay – ice flowing over the moraine at the northern reaches of the bay.

While surveying along transects in both areas, two observers using 10x binoculars recorded all marine birds and mammals observed within 100 m to either side of and in front of the 7 m survey vessel traveling at 10-15 km/h. We assumed 100% detection within the 200 m wide survey strip; observers were thoroughly trained in Murrelet identification and in distance estimation. We entered sighting and behavior data in real time onto a laptop computer running Program dLOG (Glenn Ford Consulting Inc., Portland, OR). A connected handheld GPS unit (Garmin GPSMAP-76) stamped each sighting with geographical coordinates as well as documenting the path of the survey vessel. Flying Kittlitz's Murrelet observations were not included in our habitat use analysis as we were unable to determine the exact location where they flew.

3.3.2.2 At-sea water column sampling

After completing each transect, we returned along transect to deploy the Conductivity-Temperature-Depth (CTD) meter (SBE 19 SEACAT, Sea-Bird Electronics Inc, Bellevue, Washington). In Harriman Fjord, cast locations for CTD water column sampling were separated by 400 m; cast locations in Heather Bay were separated by 200 m (Fig. 3.2.) All CTD casts were completed within 1.5 hours of the end of the survey for that transect. The CTD meter was suspended just below the surface and allowed to equilibrate for two minutes before being lowered to within two meters of the ocean floor. Depths at each cast point were determined by an on-board Lowrance depth finder (LMS-

350A, Lowrance: Tulsa, Oklahoma). We set the sampling rate of the CTD meter to sample water temperature, salinity, density, and depth twice per second.

We used Seabird Electronics Data Processing software (version 7.16, Seabird Electronics, Inc.) to process the raw CTD data files. First, we split the data into upward and downward portions of the casts. Next, we filtered the data from the downward portion of the cast to smooth rapidly changing data over a forward and backward gradient (Seabird Electronics 2010). We used only data from down casts because these data were collected before the water column was disturbed by the passage of the CTD meter.

We truncated the temperature-depth data at 25 m depth based upon foraging studies of the closely related Marbled Murrelet (*Brachyramphus marmoratus*). Marbled Murrelets generally dive <20 m, and only occasionally reach depths >30 m (Jodice and Collopy 1999). In addition, the average dive time of Kittlitz's Murrelets foraging in Harriman Fjord in 2009 was 22 s (95% CI = 18.5-25.4), suggesting individuals do not typically dive deep in these areas (Allyn et al., unpubl. data). We estimated surface temperatures using the average water column temperatures recorded during the equilibration period when the CTD was roughly 1 m below the surface. Finally, because we were interested in relative temperature profile patterns rather than absolute temperatures, we subtracted each recorded temperature from the surface temperature for that cast.

3.3.2.3 Spatial landscape features

We calculated spatial landscape feature values for both used and available locations. We defined “used habitat” as the longitude and latitude location recorded for each Kittlitz's Murrelet observed on surveys, and “available habitat” as the area

encompassing all transects surveyed during each individual visit to the fjord. Therefore, the available habitat area varied between visits to a fjord. We sampled the available habitat by creating a 100 x 100 m grid over each fjord using ArcGIS v. 9.3 (ESRI 2008); we then extracted the latitude and longitude centroid for each grid cell and used these locations to represent available habitat. We used Program R (R Core Development Team 2010) to calculate five spatial landscape features for each used and available location: water depth, and distances to shoreline, glaciers, moraines, and freshwater streams/outflows. We created a water depth raster layer from a PWS bathymetry ASCII file (resolution: 200 m) (Kiefer et al. 2008). Using this bathymetry file in combination with NOAA charts, we also identified submerged moraines as shallow (0-30 m) arms extending into and/or across fjords/bays. Satellite images (U.S. Geological Survey Global Visualization Viewer Landsat Archive) from July 2009 provided the terminus location of each tidewater glacier. We defined the shoreline and locations of freshwater streams using a data layer provided by the U.S. Forest Service (USDA Forest Service 2008a, USDA Forest Service 2008b). We interpolated depth values for each used and available point from the bathymetry raster file (Kiefer et al. 2008) using the inverse distance weighting function in the gstat package (Pebesma 2004). We used the nncross function in the spatstat package (Baddeley and Turner 2005) for all distance calculations. We used the shortestPath function in the gdistance package (van Etten 2011) for all over-water distance calculations. We restricted distances to the over-water distance between a point and landscape feature (glaciers, moraines and outflow regions) by setting the land conductance value to 0 and the ocean conductance value to 1.

3.3.3 Data Analysis

3.3.3.1 At-sea surveys: Kittlitz's Murrelet abundance, time of day, and tide height

We modeled Kittlitz's Murrelet abundance within Harriman Fjord and Heather Bay as a function of time of day and tide height (m) using a generalized linear model (GLM) with a Poisson error distribution and log link. We used the abundance model to investigate the influence of time of day and tide on predicted counts of Kittlitz's Murrelets, independent of temperature-depth profile and landscape features. This allowed us to then use the full collection of CTD casts collected during a visit in characterizing the available habitat with regards to temperature-depth profile structures, as described below.

We calculated Kittlitz's Murrelet abundance by summing the number of Kittlitz's Murrelets counted during 15-min intervals. We calculated the time of day for each observation as the median time per 15-min interval from the associated time stamp output from the program dLOG and the attached GPS device. We used height from mean high tide (m) data (NOAA Tides and Currents - http://co-ops.nos.noaa.gov/tide_predictions.shtml) to calculate the average tide height for each 15-min time interval. We used tide height data from Passage Canal predictions (~35 km to the southwest) for Harriman Fjord, and Port Valdez predictions (~40 km to the northeast) for Heather Bay tide heights. Our full abundance model was:

$$\text{Log}(p) = \alpha + \beta_1 * \text{time.of.day} + \beta_2 * \text{avg.tide.height} \quad (3.1)$$

3.3.3.2 Temperature-depth profiles

After processing the temperature-depth CTD data, we summarized the data by calculating an individual deviance value from the observed temperature-depth profile and a number of candidate temperature-depth profiles. This process allowed us to reduce CTD temperature-depth measurements into one usable metric that could be included as a variable in our habitat use model. We used a piece-wise linear function with three segments to create candidate temperature-depth profiles. Specifically, we varied the slope of the three segments by changing the depth and temperature between the start and end of each segment, resulting in a total of 1500 candidate temperature-depth profiles (Table 3.2). For an individual candidate temperature-depth profile and CTD cast, we calculated residuals at each observed depth by subtracting the relative observed temperature to the predicted temperature calculated using the piece-wise linear function. Lastly, we summed all squared residual values and divided by the number of samples (i.e., observed depths) to calculate an overall cast deviation value for an individual candidate temperature-depth profile.

The CTD data, and therefore cast deviation values, varied with time of day and tide height within a given survey and moreover did not correspond temporally with the Kittlitz's Murrelet observations since the casts were taken after the Murrelet surveys were completed. This temporal variability created a problem in calculating an average temperature-depth profile habitat value for each survey that would meaningfully represent available habitat for each Kittlitz's Murrelet observation. If we simply averaged cast deviation values without accounting for this variability, this would assume temperature-depth profiles were constant throughout the entire sampling period and that

all Kittlitz's were exposed to the same available habitat conditions regardless of when they were observed. This is not the case given the influence of time of day and tide on water column characteristics and currents and the temporal distribution of Kittlitz's Murrelets. Unfortunately, the detail in our CTD data set was not adequate for modeling changes in the temperature-depth profile as a function of time and tide. Consequently, we used our bird observation data and the resulting Poisson abundance model (Eq. 3.1) to quantify the relationship between mean predicted Kittlitz's Murrelet count, time of day, and tide. Using this function to weight cast deviation values, we were able to use all CTD casts collected throughout the day to calculate an average temperature-depth profile that we assumed represented the range of temperature-depth profiles available to birds within a given survey, over the course of the sampling period.

Specifically, for a given temperature-depth profile, and therefore deviance measurement for each cast and candidate temperature-depth profile, we multiplied the deviation values by the predicted mean Kittlitz's Murrelet count given the time of day the cast was completed, resulting in a weighted deviation. We summed all weighted deviations by day, and divided the sum of all weighted deviations by the sum of all predicted mean Kittlitz's Murrelet counts. This yielded a weighted average deviation that accounted for the variation in mean predicted Kittlitz's Murrelet counts dependent on time of day and tide height. The weighted average deviation was unique for each individual visit to a fjord.

We calculated the temperature-depth profile deviation value at used points with the inverse distance weighting function in the *gstat* package (Pebesma 2004). For a given bird observation, we used only CTD casts collected along the same transect the bird was

observed on for interpolation. This yielded the most accurate estimate of the deviation value for a given use location. We repeated this procedure for each bird observation location and for all candidate temperature-depth profiles.

3.3.3.3 Kittlitz's Murrelet habitat use

We paired the habitat measures for each used point with the average value among available points within the same fjord to investigate Kittlitz's Murrelet habitat use. For temperature-depth profile structures, we subtracted the weighted average deviation from the interpolated temperature-depth profile values at used points, by day. Temperature-depth profile structures with an average positive difference from interpolated temperature-depth profiles were removed from consideration because these proposed temperature-depth profiles represented candidate structures that fit available locations well, but poorly described the temperature-depth profiles at locations used by Kittlitz's Murrelets. In other words, for an average positive difference to occur for a given candidate profile, the deviance between the candidate structure and the profile at Kittlitz's Murrelet use locations must be greater than the average weighted deviance across all cast stations. Contrastingly, average negative differences indicated that the deviation between the candidate structure and the temperature-depth profile at Kittlitz's Murrelet use locations was smaller than the deviation between the candidate structure and the average available habitat temperature-depth profile.

For landscape features, we first averaged all the available habitat values for each variable within each fjord. We then subtracted each average value from the corresponding used covariate value for each location. This process generated a file

containing a line for every Kittlitz's Murrelet observation that included the difference in used and average available deviation values for each of the candidate temperature-depth profiles and the difference in used and average available values for each of the five landscape features.

We then used a GLM with a binomial error distribution, logit link function, and fixed intercept (Breslow and Day 1980) to investigate the difference in used and available Kittlitz's Murrelet habitat for temperature-depth profile and the five landscape variables. We used Firth's bias-reduction method (Firth 1993) as implemented in the *brglm* package (Kosmidis 2010), where parameters were estimated using maximum penalized likelihood. Harriman Fjord and Heather Bay were modeled separately to allow for differences between fjords that may influence temperature-depth profiles (e.g., bathymetry, glacier influences, etc.). For Harriman fjord, our full model was:

$$\text{Logit}(p) = F_1 * \text{depth} + F_2 * \text{dist.shore} + F_3 * \text{dist.glacier} + F_4 * \text{dist.moraine} + F_5 * \text{dist.stream} + F_6 * \text{temp.depth.profile} + (-1) \quad (3.2)$$

For Heather Bay our full model was:

$$\text{Logit}(p) = B_1 * \text{depth} + B_2 * \text{dist.shore} + B_3 * \text{dist.moraine} + B_4 * \text{dist.stream} + B_5 * \text{temp.depth.profile} + (-1) \quad (3.3)$$

Distance to glacier was not included in the Heather Bay GLM (Eq. 3.3) because the terminus of Columbia Glacier is located over 12 km beyond the head of Heather Bay. Consequently, we used only "distance to moraine" in the Heather Bay GLM, which was strongly correlated with distance to glacier.

We selected the best candidate temperature-depth structure by comparing negative log-likelihood values among GLMs with all landscape features while varying only the temperature-depth candidate variable. Because the number of parameters was constant across all models, the temperature-depth profile that maximized the negative log-likelihood of the GLM was used as our best estimate of the temperature-depth profile at Kittlitz's Murrelet use locations. We then investigated the full range of model subsets, using the best temperature-depth profile and all landscape feature covariates.

We suspected that GLM residuals might be spatially auto-correlated in response to the patchy distribution of Kittlitz's Murrelets in PWS. However, there is not a formal, well-established test for spatial autocorrelation of GLM residuals (R. Bivand, pers. comm.). Therefore, we inspected model residuals for spatial autocorrelation by plotting the Moran's I statistic for a range of distance bins from 0 to 2000 m. The Moran's I statistic calculates the autocorrelation among values as a function of the distance between the values, where a Moran's I statistic of either 1 or -1 indicate perfect correlation and a Moran's I of 0 indicates complete independence.

3.4 Results

3.4.1 Kittlitz's Murrelet abundance, time of day, and tide height

We observed 195 Kittlitz's Murrelets, 137 Kittlitz's Murrelets in Harriman Fjord (Fig. 3.3) and 58 Kittlitz's Murrelets in Heather Bay (Fig 3.4). Overall, the mean density (birds kilometer⁻¹) among visits was similar for the two fjords; however, the density variability among trips was considerably smaller in Harriman Fjord (mean = 23.29, SD =

16.22 birds kilometer⁻¹) than that in Heather Bay (mean = 25.33, SD = 37.72 birds kilometer⁻¹).

Although the effect of fjord was not significant (Table 3.3), both time of day and average tide height parameters were highly significant in affecting abundance in the GLM (Table 3.4). The predicted mean count of Kittlitz's Murrelets in a fjord increased with increasing tide heights, and decreased throughout the day (Fig. 3.5). AICc values suggested a slightly better model fit when an interaction between time of day and tide height was included in the GLM (Table 3.5). However, analysis of variance between the GLM including the interaction term and the GLM with no interaction term was not significant ($df = 1$, p -value = 0.053). Therefore, we chose the simple linear model (*time of day + tide height*) with no interaction between time of day and tide height as our function for weighting CTD casts.

3.4.2 Water column properties overview

Although average temperatures between Harriman Fjord (5.69 °C) and Heather Bay (5.46 °C) were very similar, there was less variability in the temperatures recorded in Harriman Fjord (range = 4.66-7.77 °C) than in Heather Bay (range = 0.78-7.89 °C) (Fig. 3.6). Additionally, in Harriman Fjord the coldest water was found at maximum depths (25 m), and in Heather Bay the coldest water was at the surface.

Overall, average salinities in Harriman Fjord (28.1 ppt) were slightly lower than those in Heather Bay (30.3 ppt) (Fig. 3.6). Further, the range in salinity values was greater in Harriman Fjord (range = 17.1 - 30.7 ppt) compared to Heather Bay (range = 21.7 - 31.4 ppt). Lastly, density profiles across CTD casts in both Harriman Fjord and Heather Bay showed increasing density with increasing water depth, where the least

dense water was always on top of more dense water masses, suggesting the relative temperature-depth patterns we observed were stable.

3.4.3 Kittlitz's Murrelet habitat use

3.4.3.1 Harriman Fjord

Overall, the best candidate temperature-depth model decreased by 2 °C relative to the surface temperature between the surface and 5 m, and then increased by 6 °C between 5 and 15 m, finally cooling with increased depth beyond 15 m (Fig. 3.7). Of the 779 proposed temperature-depth profiles, three candidate profiles were within 2 AICc units of each other (Fig. 3.7).

Before evaluating all model subsets of the global GLM, we investigated the spatial autocorrelation of Kittlitz's Murrelet observations in the global GLM residuals. The plot of spatial autocorrelation over a range of distance bins showed a dramatic decrease in Moran's I values over a very short distance (~15 m), and Moran's I values were ~0.0 when the distance bin was >50 m (Fig. 3.8). Further, <3% of the distances between paired Kittlitz's Murrelet observations were ≤ 50 m. Therefore, we proceeded to evaluate all model subsets and did not use methods to account for or remove the minimal spatial autocorrelation observed.

The best overall GLM describing Kittlitz's Murrelet habitat use in Harriman Fjord included depth, distance to shore, distance to glacier, and temperature-depth profile as model variables (Table 3.6). Kittlitz's Murrelets appeared to use locations that were shallower, further from shore, and closer to Surprise Glacier than the average available habitat (Table 3.7, Fig. 3.9).

3.4.3.2 Heather Bay

In Heather Bay, the best candidate temperature-depth profile suggested Kittlitz's Murrelets used habitats where the water column temperature increased moderately relative to the surface temperature up to 5 m depth, and then decreased rapidly with increasing depths (Fig. 3.10). However, because the distribution of Kittlitz's Murrelets in Heather Bay was extremely patchy, and all Kittlitz's Murrelets were observed closer to the moraine than the average available habitat, distance to moraine masked the potential significance of temperature-depth candidate structure and the other landscape feature variables (Table 3.8).

Before removing distance to moraine from the model to investigate the relative significance of the other variables, we inspected the spatial autocorrelation of the global GLM residuals. The spatial autocorrelation in Heather Bay model residuals was similar to that observed in Harriman Fjord, where Moran's I values decreased rapidly and approached 0.0 when paired distances were >15 m (Fig. 3.8). Therefore, we continued model subset investigations without removing the small autocorrelation observed because of this rapid drop in Moran's I statistics over short distances, and because $\sim 1\%$ of the distances between paired observations were ≤ 15 m.

After removing the highly significant distance to moraine variable from the model, both water depth and distance to shore became significant parameters describing Kittlitz's Murrelet habitat use in Heather Bay. Kittlitz's Murrelets appeared to use shallower waters at locations closer to shore than the average available (Table 3.9, Fig. 3.11). The candidate temperature-depth profile variable remained insignificant, and there was no clear association between locations used by Kittlitz's Murrelet and distance to freshwater outflow areas (Table 3.9, Fig. 3.11).

2.5 Discussion

Similar to the findings of previous broader extent studies in PWS (Day et al. 2003, Kuletz et al. 2003, Stephensen 2009), our results indicate that Kittlitz's Murrelets used shallow waters close to the face of tidewater glaciers, glacial outflow regions, and moraines. In Harriman Fjord, we found that temperature-depth profile significantly influenced Kittlitz's Murrelet habitat use. Although the temperature-depth profile variable was insignificant in Heather Bay, likely due to our small sample size, the best candidate temperature-depth profile selected using negative log-likelihood values does suggest that the temperature-depth profiles at locations used by Kittlitz's Murrelets were markedly different between fjords.

The temperature-depth profiles in both fjords appear to be driven by landscape structure and transport dynamics. The bottom topography within the sampled region of Harriman Fjord is highly variable and includes a glacial moraine. This moraine appears to facilitate tidal upwelling. On an incoming tide, warmer, more saline ocean waters enter over the moraine and force the relatively cooler, fresher and more glacially-influenced waters towards the surface as they converge. This phenomenon was evident in the data as a cold wedge at shallow depths (Fig. 3.12), prominent at most Kittlitz's Murrelet use locations. This association with moraine upwelling events is further evidenced by the higher occurrence of Kittlitz's Murrelets with higher tidal heights.

In contrast to the sampling region in Harriman Fjord, Heather Bay contains no tidewater glaciers. However, the fjord is still strongly influenced by Columbia Glacier in neighboring Columbia Bay. Columbia Glacier is currently in drastic retreat (Walter et al. 2010) and produces a large volume of icebergs calved from its receding face. A

submerged moraine 6.5 km from the mouth of Columbia Bay serves as a dam, creating a densely packed pool of trapped icebergs ~12 km long. At the head of adjoining Heather Bay, an intertidal moraine separates Columbia's iceberg pool from the warmer waters of Heather Bay. These calved icebergs, combined with the cold (~1 °C) pool water, breach the Heather Bay moraine during each incoming tide and pour into Heather Bay. In striking contrast to the observed upwelling in Harriman Fjord, the cold, fresh glacial water enters and remains at the surface of the water column in Heather Bay (Fig. 3.13). This temperature-depth profile best matched locations where we observed Kittlitz's Murrelets within Heather Bay, where surface waters were dramatically cooler than underlying water.

The influence of temperature-depth profiles on Kittlitz's Murrelet habitat use is most likely the result of prey distributions as affected by water column characteristics. Temperature gradients can affect the distribution of fish and zooplankton (e.g., Abookire et al. 2000, Coyle & Pinchuk 2005, Speckman et al. 2005), and create concentrations of prey within and slightly above or below water masses of different temperatures (e.g., Haney 1988, Frank et al. 1989, Hunt 1990). Additionally, in glacial fjord systems macrozooplankton species may avoid the colder, less saline, more turbid waters when entering the system, resulting in high concentrations of macrozooplankton near these interface points (Weslawski et al. 1995). Therefore, the interface between water masses may aggregate prey species not only at certain locations within the fjord, but also at certain depths and times (i.e., tidal phases) at particular locations. These distinct patterns could ultimately allow Kittlitz's Murrelets, known to be "persistent hotspot" foragers (Day & Nigro 2000, Stephensen 2009), to focus their foraging efforts on predictable prey hotspots both spatially within the fjord and vertically within the water column.

A substantial proportion of the remaining global population of Kittlitz's Murrelets is found in the glacial fiords of PWS during the summer months (USFWS 2010, Kuletz et al. 2011). Within PWS, Harriman Fjord and Heather Bay can host relatively high densities of this rare seabird (Kuletz et al. 2011). Our research shows that entirely different dynamics may be at play in rendering each of these areas a reliable Kittlitz's Murrelet foraging hotspot. Both systems, however, are heavily dependent on glacial input. Considering more than 98% of tidewater glaciers in Alaska are now receding (Molnia 2007), glacial influence on these important Kittlitz's Murrelet refugia is likely to change significantly in coming decades. Given the tight association between Kittlitz's Murrelets and glacial features, reduction in the effects of glacial influx on the water column in fjords will likely degrade the quality of Kittlitz's Murrelet habitat. For a species with already low overall population numbers, further reductions in survival or productivity rates from a reduction in foraging habitat quality could prove devastating to future Kittlitz's Murrelet populations.

3.6 Acknowledgements

The Earthwatch Institute provided funding for this project, and the U.S. Fish and Wildlife Service Migratory Bird Management Program-Anchorage, AK provided survey vessels and equipment. We thank Alex Robbins and Nick Nelson for their dedicated field support and help with data collection. Additionally, we thank the Earthwatch volunteers, Amanda Adley, Samantha Arthur, David Brindle, Mario Rivera, Dan Smith, Rebecca Speer and Julie Stayner, for their help with data collection. Drs. Mark Leckie and Julie Brigham-Grette provided helpful insight into interpreting temperature-depth profiles, and possible tidewater glacier mechanisms, which could have caused the observed profiles.

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Table 3.1. Date, area, Kittlitz's Murrelet density region, number of transects surveyed, and conductivity-temperature-depth (CTD) casts completed in Heather Bay and Harriman Fjord, Alaska, July 2008.

Fjord –			
Date	Kittlitz’s Murrelet density region	Number of transects	Number of CTD casts
2 July	Heather Bay - High	4	17
5 July	Heather Bay - Low	4	23
10 July	Harriman Fjord - High	2	12
	Harriman Fjord - Low	2	9
17 July	Harriman Fjord - High	4	13
20 July	Heather Bay - High	7	13
	Heather Bay - Low	4	10
26 July	Harriman Fjord - High	3	8
	Harriman Fjord - Low	2	7

Table 3.2. Parameter descriptions and range of possible values used in constructing candidate temperature-depth profile models with linear piece-wise function.

Parameter	Possible values
Temperature at 1 st inflection	0, 2, -2, 4, -4
Depth at 1 st inflection	2.5, 5, 7.5, 10
Temperature at 2 nd inflection	0, 2, -2, 4, -4
Depth at 2 nd inflection	10, 15, 20
End temperature	0, 2, -2, 4, -4
End depth	25

Table 3.3. Point estimates, standard errors (SE) and probability values (P) of parameters included in generalized linear model describing Kittlitz's Murrelet abundance, with fjord as a factor, in Heather Bay and Harriman Fjord, Alaska, July 2008.

Parameter	Estimate	SE	z value	P (> z)
Intercept	3.16	0.58	5.42	5.92×10^{-8}
Time of day	-0.29	0.04	-6.6	4.18×10^{-11}
Average tide height	0.43	0.06	7.71	1.3×10^{-14}
Fjord (factor)	-0.39	0.21	-1.85	0.06

Table 3.4. Point estimates, standard errors (SE) and probability values (P) of parameters included in the generalized linear model describing Kittlitz's Murrelet abundance in Heather Bay and Harriman Fjord, Alaska, July 2008.

Parameter	Estimate	SE	z value	P ($> z $)
Intercept	2.63	0.50	5.29	1.22×10^{-7}
Time of day	-0.27	0.04	-6.51	7.68×10^{-11}
Average tide height	0.43	0.06	7.69	1.48×10^{-14}

Table 3.5. Model description and AICc values for generalized linear models, with and without an interaction term, describing Kittlitz's Murrelets abundance in Heather Bay and Harriman Fjord, Alaska, July 2008.

Model	AICc
intercept + time.of.day + avg.tide.height + time.of.day*avg.tide.height	220.42
intercept + time.of.day + avg.tide.height	221.93

Table 3.6. Descriptions of the best ten models as selected by AICc, including AICc values, ΔAICc , and Akaike model weights (w), describing Kittlitz's Murrelet habitat use in Harriman Fjord, Alaska, July 2008.

Model	AICc	ΔAICc	w
depth+ distance to shore + distance to glacier + temperature.depth profile	34.53	0	0.508
depth+ distance to shore + distance to glacier + distance to moraine + temperature.depth profile	36.19	1.66	0.222
depth + distance to shore + distance to glacier + distance to stream + temperature.depth profile	36.91	2.38	0.155
depth + distance to shore + distance to glacier + distance to moraine + distance to stream + temperature.depth profile	38.37	3.84	0.075
depth + distance to glacier + distance to stream + temperature.depth profile	42.91	8.38	0.008
depth + distance to shore + temperature.depth profile	43.41	8.88	0.006
depth + distance to glacier + temperature.depth profile	43.87	9.34	0.005
depth + distance to glacier + distance to moraine + temperature.depth profile	44.32	9.79	0.004

depth + distance to glacier + distance to moraine + distance to stream	44.61	10.08	0.003
+ temperature.depth profile			
depth + temperature.depth profile	45.02	10.49	0.003

Table 3.7. Point estimates, standard errors (SE) and probability values of parameters included in the best generalized linear model as selected by AICc describing Kittlitz's Murrelet habitat use in Harriman Fjord, Alaska, July 2008.

Parameter	Estimate	SE	z value	P (> z)
Depth	0.17	0.06	3.05	0.002
Distance to shore	7.16	2.96	2.42	0.01
Distance to glacier	-1.03	0.38	-2.71	0.007
Temperature-depth profile	3.64	1.4	2.60	0.009

Table 3.8. Point estimates, standard errors (SE), and probability values (P) of parameters included in the global generalized linear model describing Kittlitz's Murrelet habitat use in Heather Bay, Alaska, July 2008.

Parameter	Estimate	SE	z value	P (> z)
Depth	-0.02	0.04	-0.36	0.72
Distance to shore	-2.06	6.99	-0.29	0.77
Distance to moraine	-2.35	0.75	-3.13	0.0018
Distance to stream	-0.39	2.56	-0.15	0.88
Temperature-depth profile	0.22	0.29	0.76	0.45

Table 3.9. Point estimates, standard errors (SE), and probability values (P) of parameters in the GLM without distance to moraine describing Kittlitz's Murrelet habitat use in Heather Bay, Alaska, July 2008.

Parameter	Estimate	SE	z value	P (> z)
Depth	0.3	0.12	2.59	0.0099
Distance to shore	-16.12	6.75	-2.39	0.017
Distance to stream	-0.39	1.72	-0.22	0.82
Temperature-depth profile	0.09	0.33	0.29	0.77

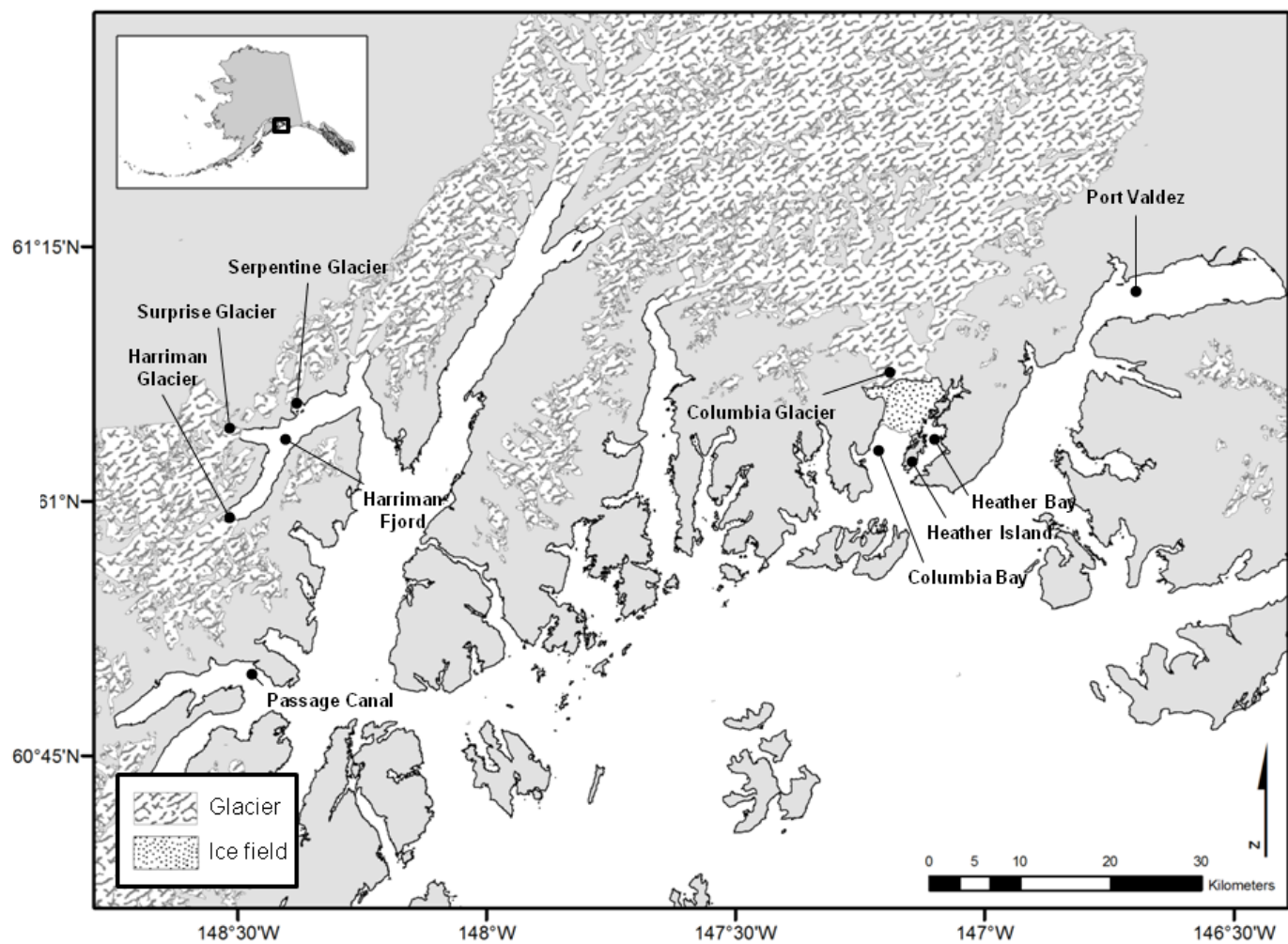


Figure 3.1. Northern Prince William Sound, Alaska showing Heather Bay and Harriman Fjord study areas and relevant landscape features.

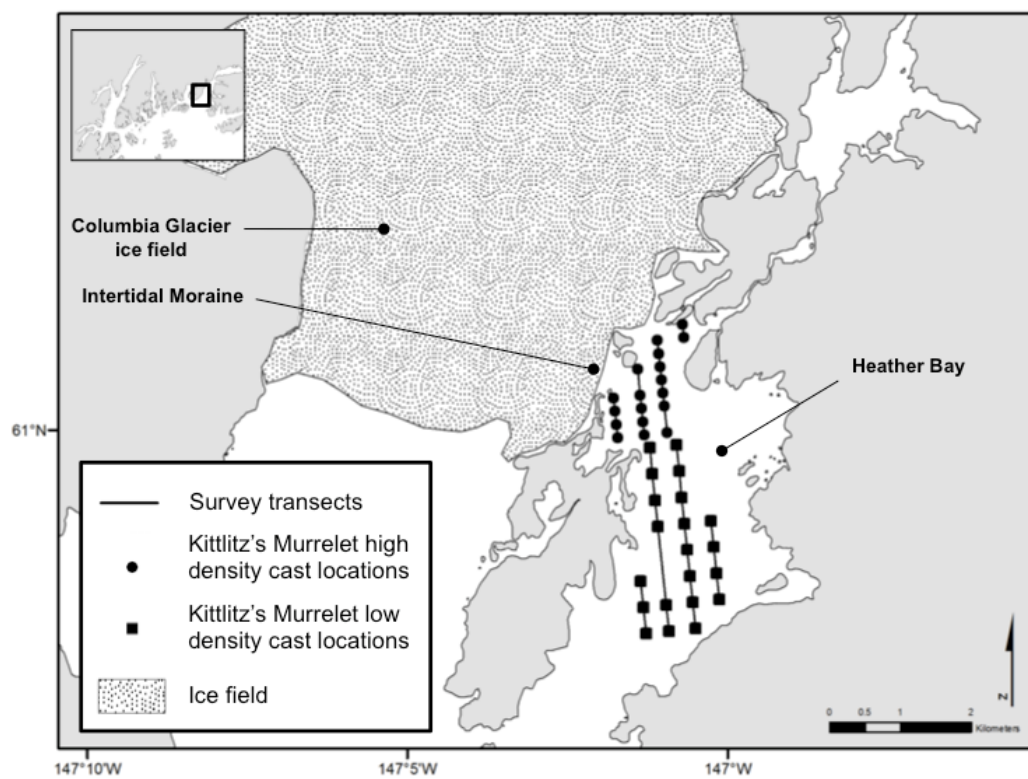
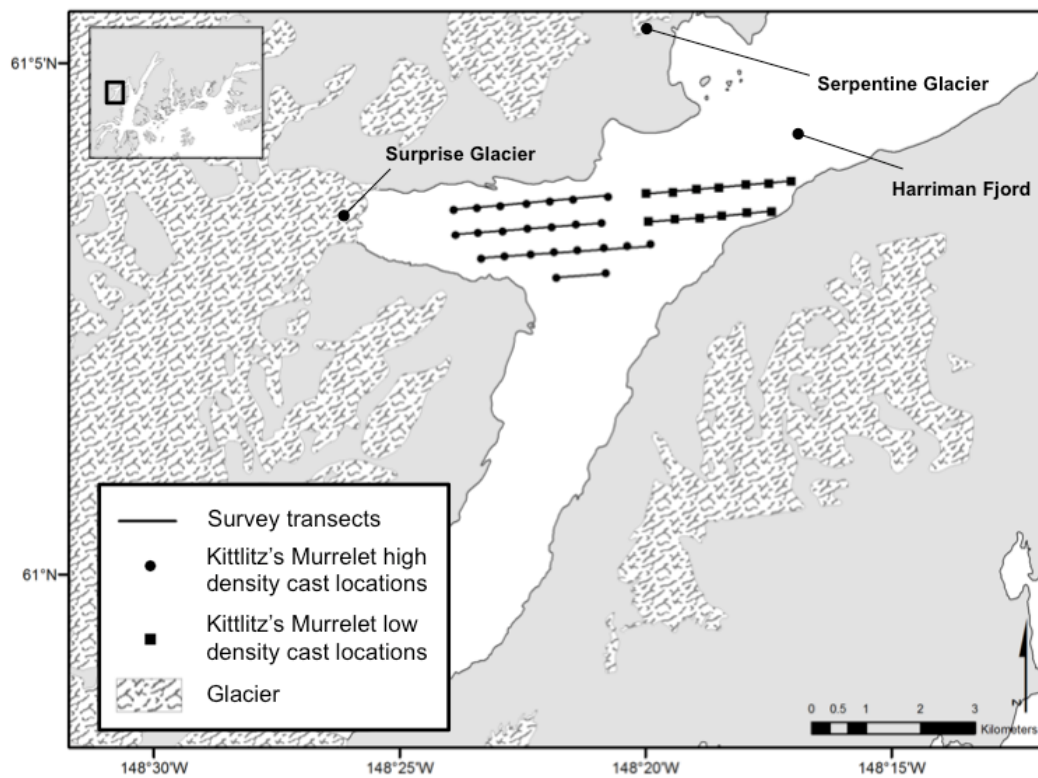


Figure 3.2. Survey transects, Kittlitz's Murrelet high (filled circles) and low (filled squares) density conductivity-temperature-depth (CTD) cast locations in Harriman Fjord (Top) and Heather Bay (Bottom), Prince William Sound, Alaska, July 2008.

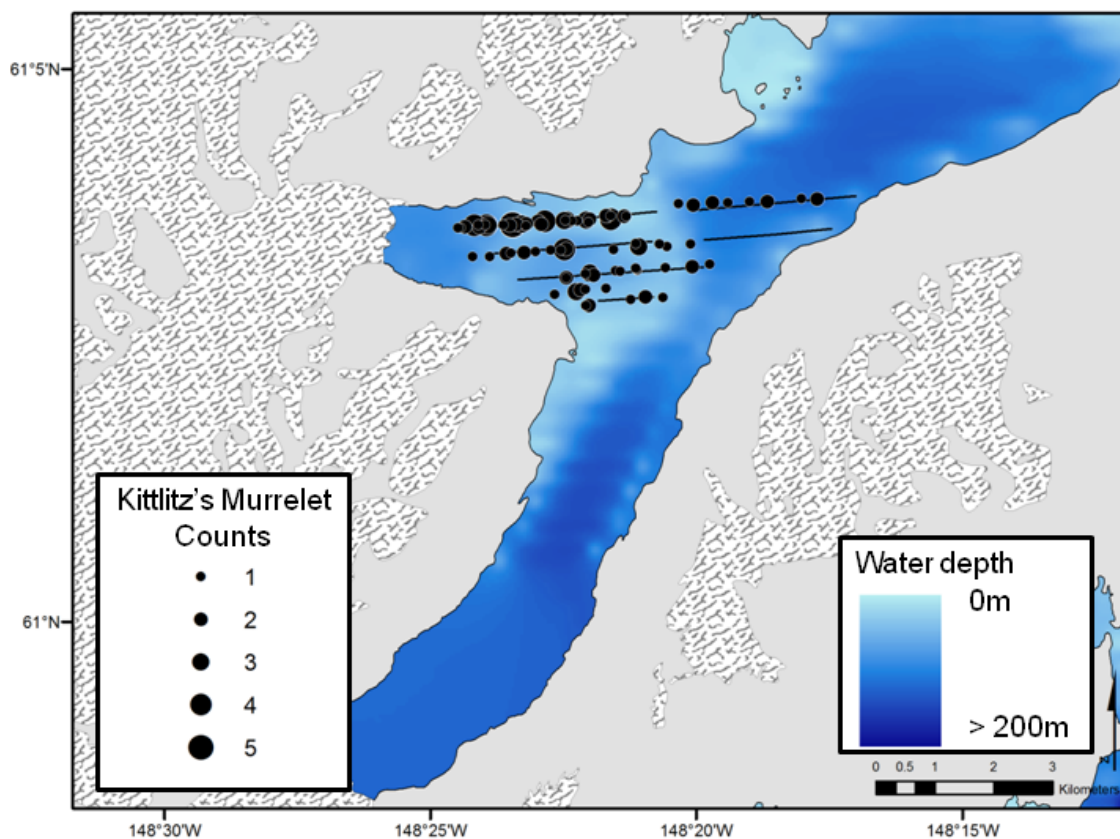


Figure 3.3. Distribution and abundance of Kittlitz's Murrelets observed on three surveys in Harriman Fjord, Alaska, July 2008.

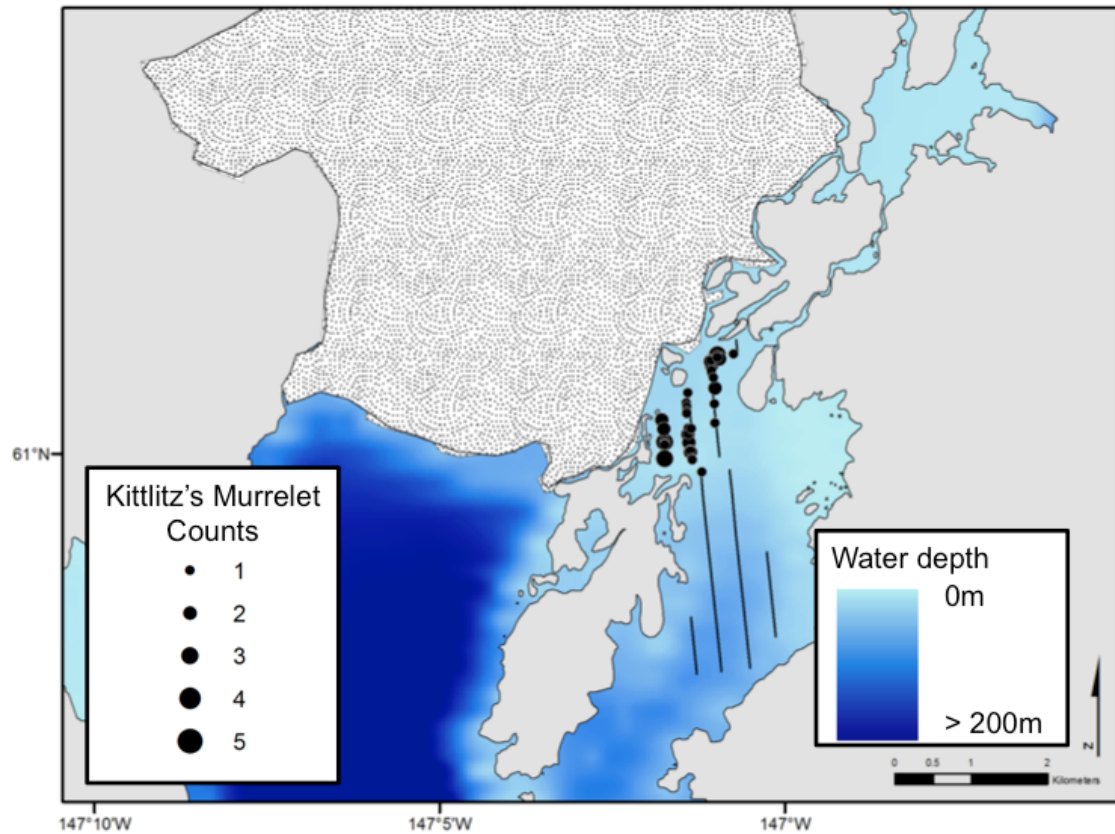


Figure 3.4. Distribution and abundance of Kittlitz's Murrelets observed on three surveys in Heather Bay, Alaska, July 2008.

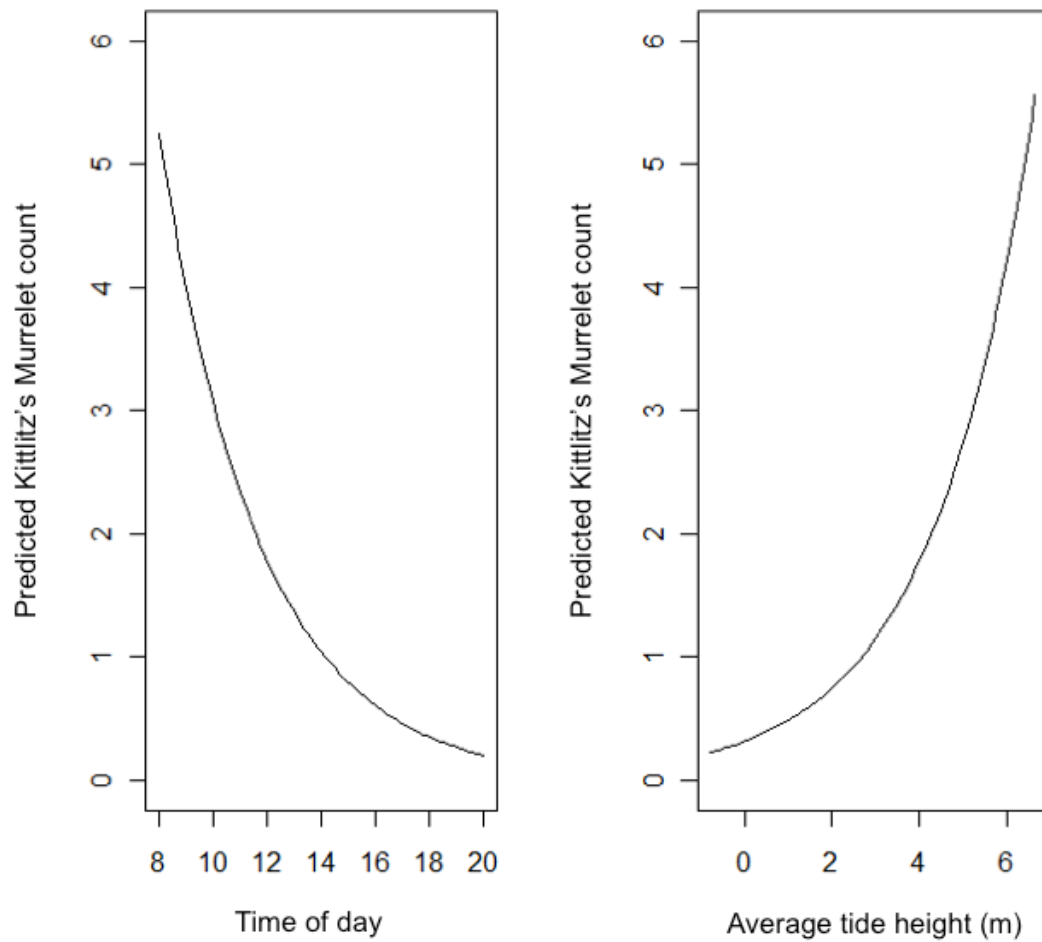


Figure 3.5. Generalized linear model predictions of the relationship among Kittlitz's Murrelet abundance, time of day and average tide height (meters) in Harriman Fjord and Heather Bay, Alaska, July 2008. Predicted Kittlitz's Murrelet counts were calculated by varying one variable across the range of its observed values and holding the other variable at its mean.

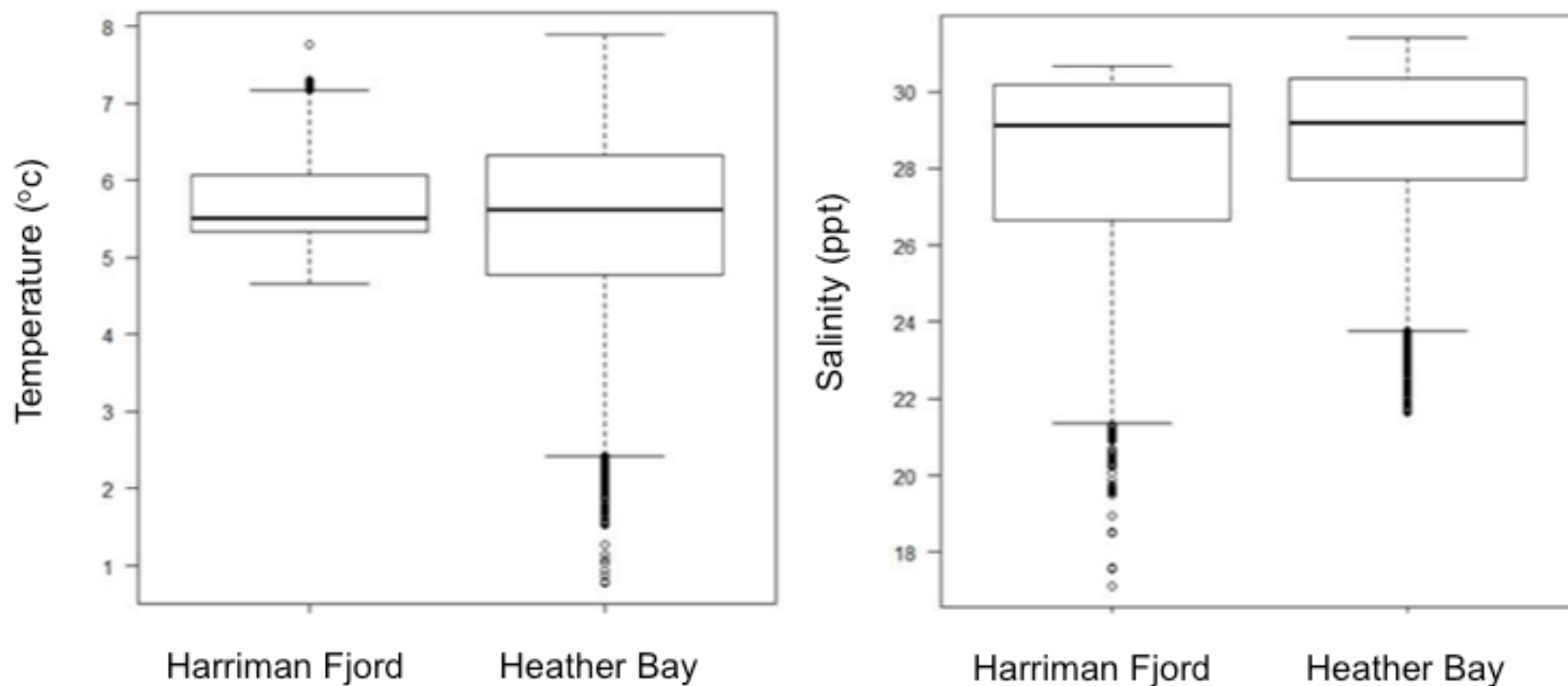


Figure 3.6. Summary plots of Heather Bay and Harriman Fjord temperature and salinity values recorded on conductivity-temperature-depth casts during surveys in Heather Bay and Harriman Fjord, Alaska, July 2008. Horizontal lines within boxes indicate data median, rectangle boxes indicate the interquartile ranges (i.e. 50% of the data), whiskers indicate extreme values out to a maximum of 1.5 times the interquartile range, data points outside these range are indicated by open circles.

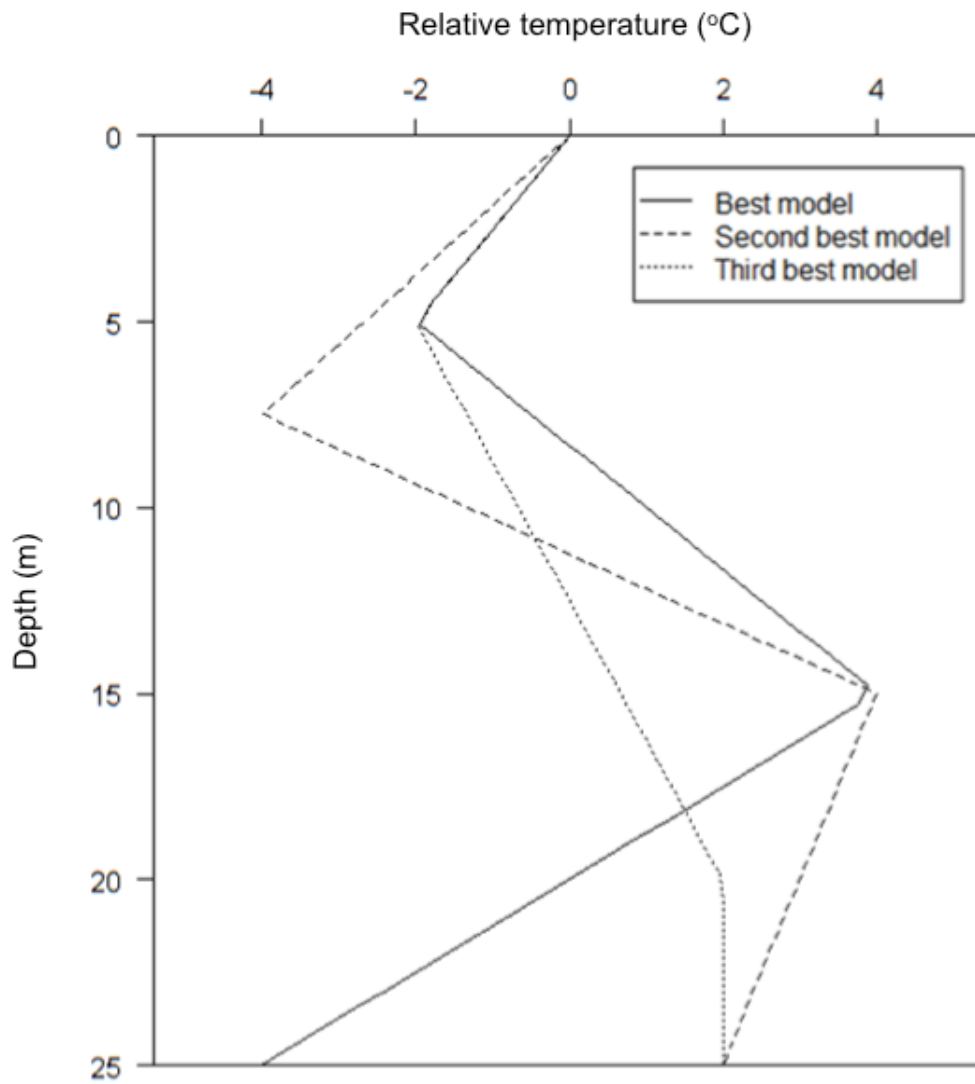


Figure 3.7. Best three candidate temperature-depth profiles, as selected by models within 2 AICc units of the best overall model, describing Kittlitz's Murrelet habitat use in Harriman Fjord, Alaska, July 2008.

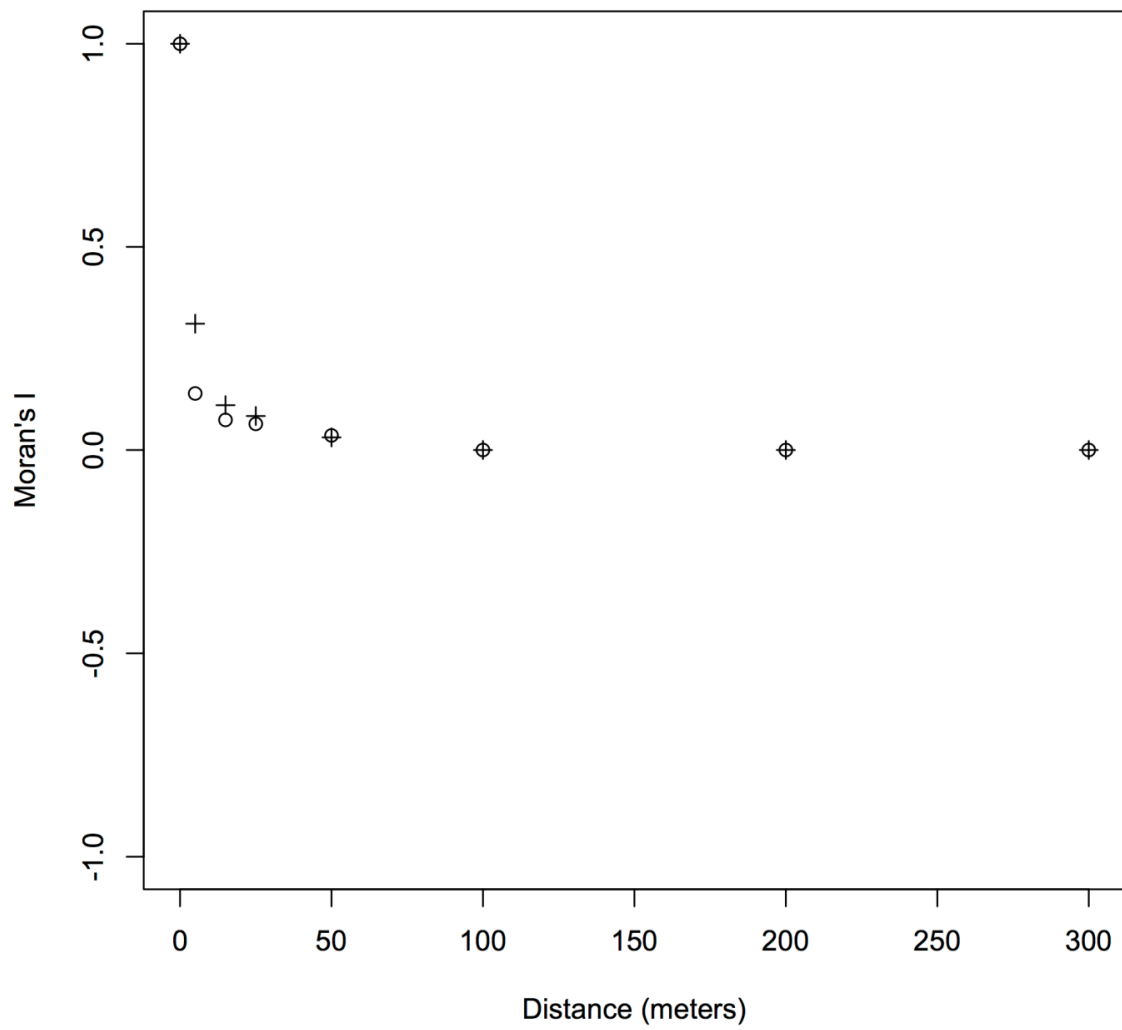


Figure 3.8. Moran's I values of generalized linear model residuals describing Kittlitz's Murrelet habitat use in Harriman Fjord (open circles) and Heather Bay (black crosses), Alaska, July 2008. Moran's I values were calculated for distance bins of 0, 5, 15, 25, 50, 100, 200, and 300 meters.

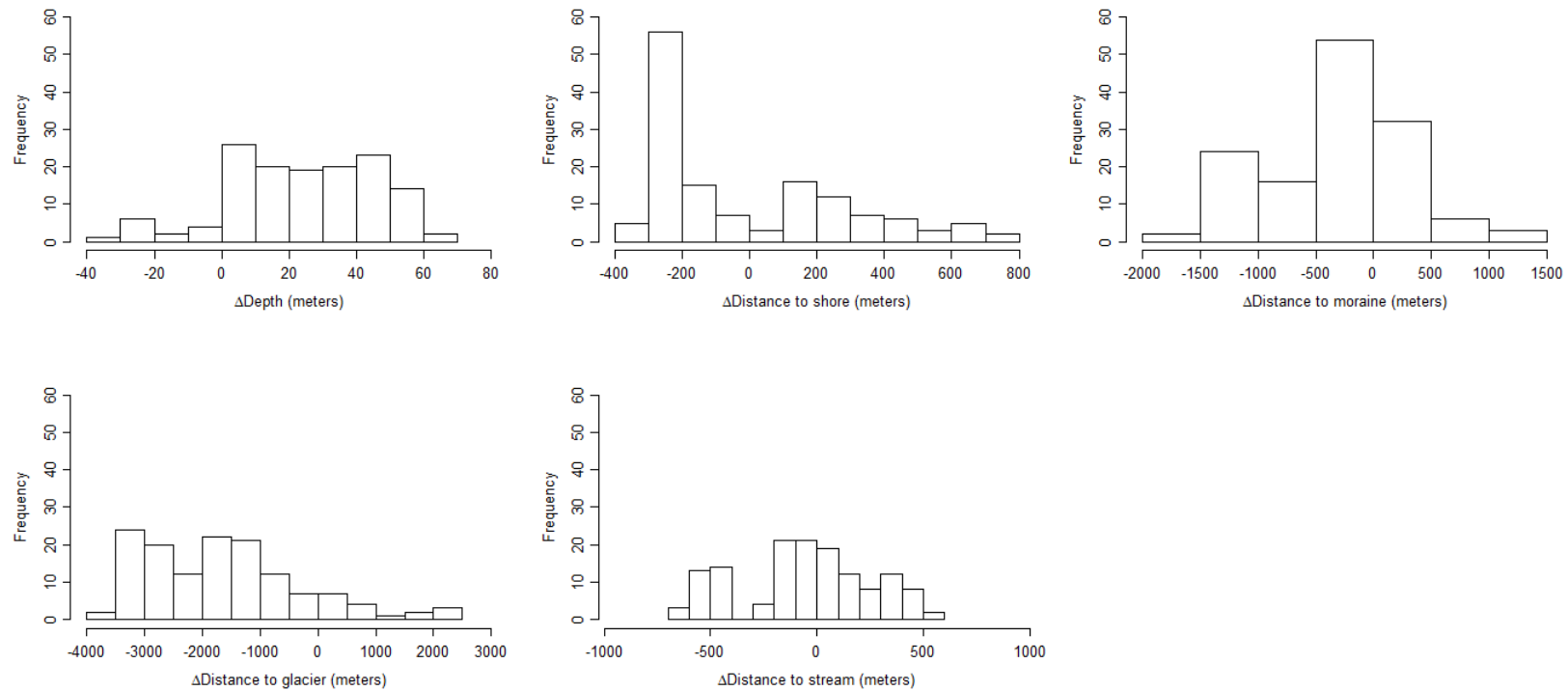


Figure 3.9. Frequency distributions of the differences between Kittlitz's Murrelet habitat use locations and average available habitat values for five landscape feature variables within Harriman Fjord, Alaska, July 2008.

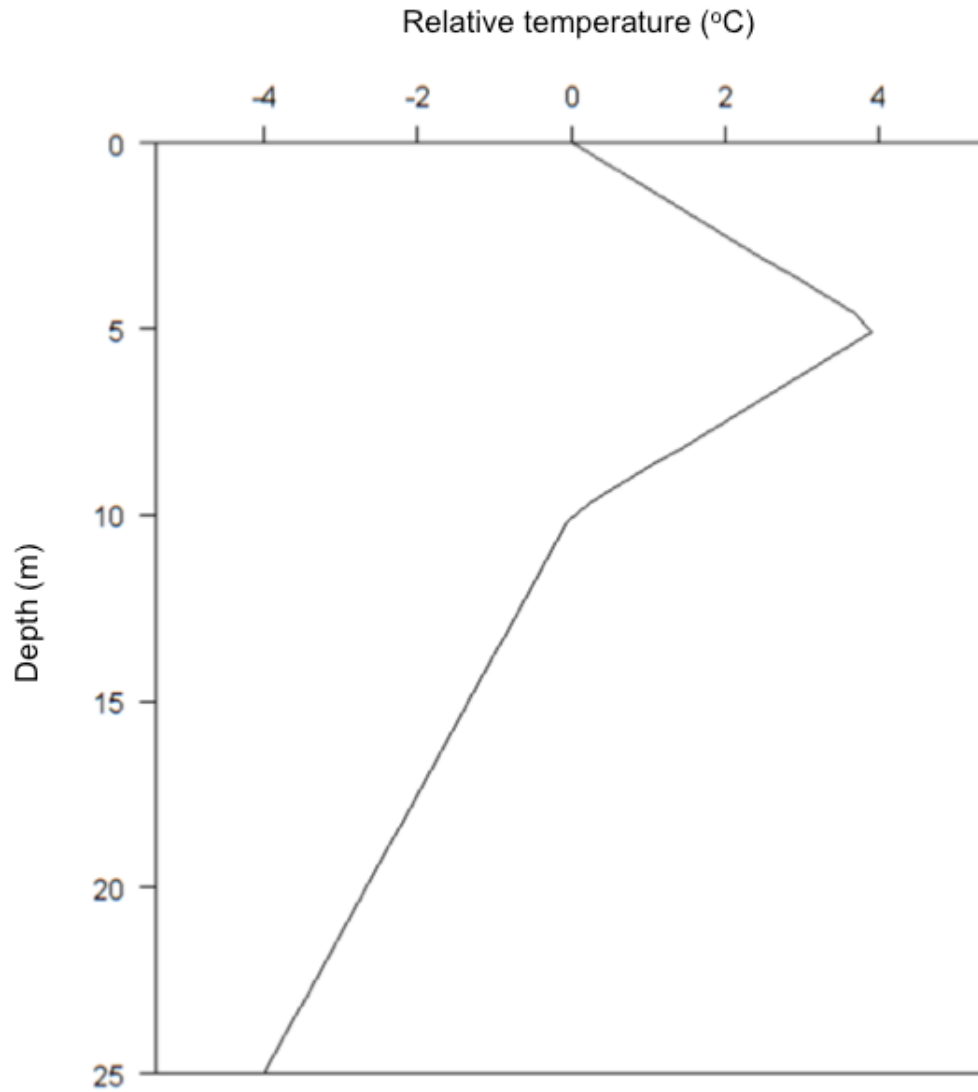


Figure 3.10. Best candidate temperature-depth profile as selected by negative log-likelihood describing Kittlitz's Murrelet habitat use in Heather Bay, Alaska, July 2008.

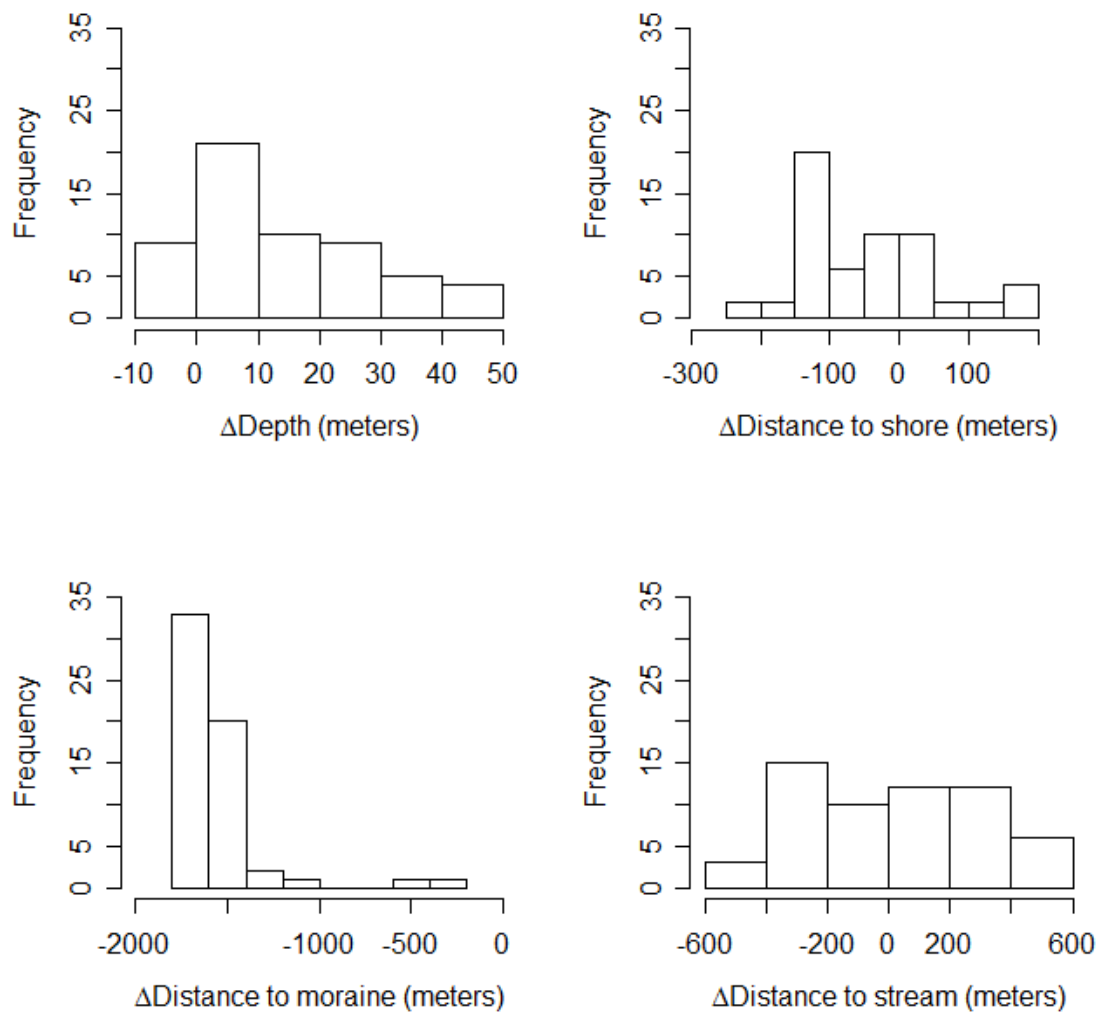


Figure 3.11. Frequency distributions of the differences between Kittlitz's Murrelet habitat use locations and average available habitat values for five landscape feature variables within Heather Bay, Alaska, July 2008.

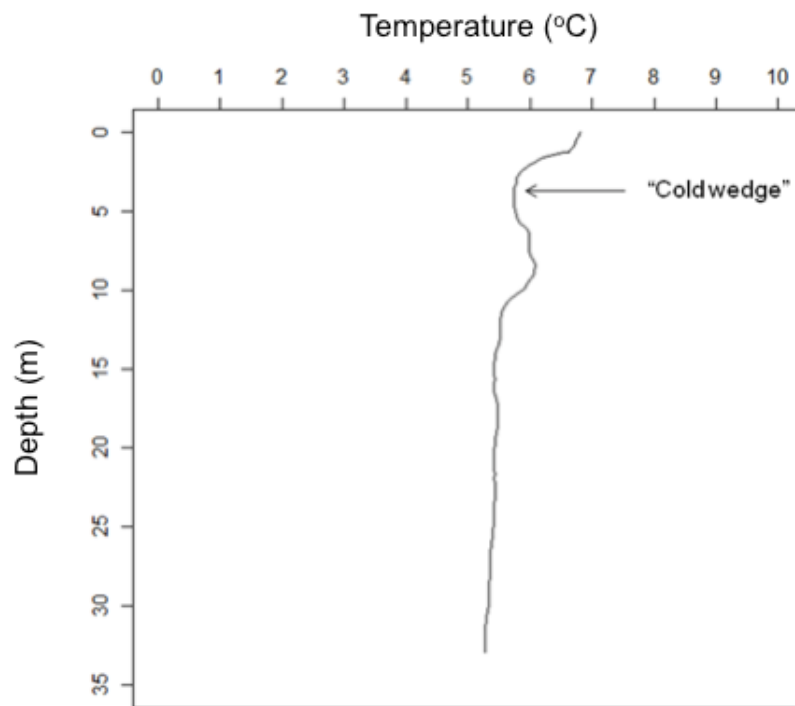


Figure 3.12. Example raw conductivity-temperature depth data from a cast in Harriman Fjord showing the characteristic “cold wedge” prevalent in all top models describing Kittlitz’s Murrelet habitat use in Harriman Fjord, Alaska, July 2008.

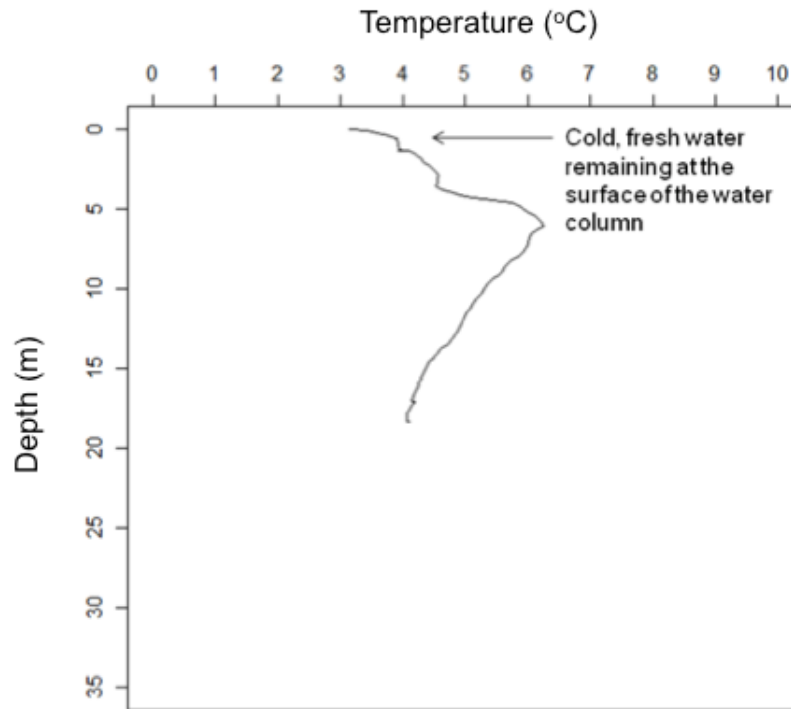


Figure 3.13. Example raw conductivity-temperature-depth data from a cast in Heather Bay showing the cold, fresh water layer remaining at the surface of the water column, prevalent in the best model describing Kittlitz's Murrelet habitat use in Heather Bay, Alaska, July 2008.

CHAPTER 4

FORAGING ECOLOGY OF KITTLITZ'S MURRELETS

IN NORTHWESTERN PRINCE WILLIAM SOUND, ALASKA

4.1 Abstract

We investigated the foraging ecology of the Kittlitz's Murrelet (*Brachyramphus brevirostris*) using a combination of stable isotope techniques and radio telemetry in northwestern Prince William Sound, Alaska in 2009. During the early breeding season, Bayesian isotope mixing model results suggested individuals foraged on a combination of zooplankton and fish. During the post-breeding season, demersal fish and near-surface pelagic fish, possibly from the Bering Sea, dominated Kittlitz's Murrelet diet. There was significantly less variation in post-breeding samples, suggesting that the post-breeding diet is more specialized than the early breeding season diet, possibly the result of the birds' flightless status during this time. We found no significant difference in isotope signatures between sexes within either season. Radio-tagged individuals foraged in rapid bouts with short dives and rests, punctuated by longer loafing periods. Taken as a whole, our results suggest that Kittlitz's Murrelets may be highly dependent on predictable foraging hotspots, especially given the constraints imposed both during the breeding season and the post-breeding molting period.

Key Words

Brachyramphus brevirostris, foraging ecology, Kittlitz's Murrelet, stable isotopes, radio telemetry, seabird

3.2 Introduction

Foraging seabirds must search heterogeneous marine environments for prey and continually balance energetic demands. As prey becomes less available, seabirds can adjust their foraging behavior by increasing time spent foraging (Cairns 1987, Montevecchi 1993, Furness 1996, Monaghan 1996), altering foraging locations (Hamer et al. 1993, Monaghan et al. 1994, Suryan et al. 2000), and shifting to different prey species (Croxall et al. 1999, Suryan et al. 2000, Litzow et al. 2002). Seabirds, however, may not be able to buffer against larger spatial or temporal declines in quality prey availability. These broad-scale changes can have detrimental effects on the survival and productivity of individuals (Piatt and Anderson 1996, Suryan et al. 2000), particularly among central-place foraging birds that are constrained by the need to return regularly to nest sites (Orians and Pearson 1979).

The Kittlitz's Murrelet (*Brachyramphus brevirostris*), a small diving seabird of the Alcidae family, may face foraging constraints year-round, posing additional threats to a species with widespread population declines in Alaska during recent decades (Arimitsu et al. 2011, Kuletz et al. 2011, Piatt et al. 2011). However, we know little about Kittlitz's Murrelet diet and foraging behavior, greatly inhibiting our ability to assess the vulnerability of this species to shifts in prey availability. Further, the scarcity of information on Kittlitz's Murrelet foraging ecology is exacerbated by the species' cryptic and solitary nesting behavior (Day et al. 1999, Kaler et al. 2009), making it virtually impossible to study this species using traditional colony-based diet data collection techniques (Duffy and Jackson 1986) commonly used with other seabirds. In this study, we use stable isotope sampling to investigate the diet of Kittlitz's Murrelets during the breeding and non-breeding seasons, and radio telemetry to determine Kittlitz's Murrelet foraging behaviors in Prince William Sound (PWS), Alaska during the breeding season.

4.3 Methods

4.3.1 Study Area

PWS is a large, glaciated embayment located in south-central Alaska that includes 5000 km² of shoreline (marine habitat within 200 m of land) and approximately 9000 km² of water surface area. PWS is surrounded by the Chugach National Forest, which contains 21320 km² of glaciers and ice fields (Molnia 2007). There are approximately 20 tidewater glaciers that terminate in PWS (Molnia 2001). Abundant freshwater, silt and ice have profound effects on this marine ecosystem, particularly during the summer. PWS waters have a diurnal tidal cycle, and the weather is characterized by frequent cloud cover and precipitation (Wilson and Overland 1986).

We captured birds to collect stable isotope samples and attach radio tags in the northwestern region of PWS, mainly the Port Wells area (Fig. 4.1). We targeted our radio-tagged birds for foraging behavior observations, and all observations were conducted within Harriman Fjord, around Point Doran (Fig. 4.1). Harriman Fjord (61° 03'0'' N 148° 22'14'' W) is approximately 65.6 km² in total area (Molnia 2001) and influenced by six glaciers: Coxe, Barry, Cascade, Serpentine, Surprise, and Harriman glaciers (Fig. 4.1). All of these glaciers are retreating with the exception of Harriman Glacier, which was advancing during the 1990s and has since become stable (Molnia 2007). The surrounding landscape of Harriman Fjord contains many high-altitude scree slopes, which are believed to be potential nest sites for Kittlitz's (Day et al. 1999).

4.3.2 Sample collection

We captured 39 Kittlitz's Murrelets between 1 May and 24 May 2009 using the night lighting and dip netting technique (Whitworth et al. 1994). All capture methods and sampling protocols were approved by the University of Massachusetts Amherst Institutional Animal Use and Care Committee (Protocol ID: 2009-0019).

We collected two samples from each individual to measure isotope signatures. First, we collected a small blood sample (<1 milliliter) from the brachial vein. We transferred a small drop of blood to filter paper that was then sent to Zoogen Incorporated labs (Davis, CA) for sex determination. The remaining blood sample was centrifuged (Clay Adams TRIAC model 0200) at ~5000 rotations per min for 15-min to separate red blood cells from plasma. Red blood cells were then immediately frozen, and later shipped on dry ice to the Cornell Stable Isotope Laboratory (Ithaca, NY) for analysis. Next, we collected a clip from the 5th secondary feather from each individual. The 5th secondary feather clips were placed inside individual glassine envelopes, frozen, and shipped along with blood samples to the Cornell Lab for analysis.

Stable isotope signatures in predators incorporate prey information during the time of tissue synthesis (Hobson and Clark 1992). For blood samples, stable isotope information indicates prey consumed over the past two weeks; therefore, we characterized stable isotope results from blood samples as indicative of early breeding season diet. As Kittlitz's Murrelets undergo a complete pre-basic molt following the breeding season (Sealy 1977), stable isotope signatures from 5th secondary feather clips were representative of prey consumed during the post-breeding period. To compare these Kittlitz's Murrelet signatures with potential prey species, we used stable carbon and stable nitrogen signatures for a variety of prey items from published and unpublished data, including samples from PWS, Icy Bay in southeast Alaska, the Gulf of Alaska (GOA) and the Bering Sea (Table 4.1).

4.3.3 At-sea foraging behavior data collection

We attached a radio transmitter (ATS Model A4360, Advanced Telemetry Systems Inc.) between the scapulars using a modified subcutaneous anchor technique (Newman et al. 1999) without sutures (Lougheed et al. 2002) to each of 12 captured Kittlitz's Murrelets. In lieu of suturing, we used VetBond tissue adhesive (3M Animal Care Products, St. Paul, MN). Attachment of telemetry units between the scapulars reduced the amount of drag caused by the tag when diving and flying. The total transmitter mass was <3.1g, representing <3% of the bird's body mass, well within the acceptable limit proposed by Gaunt et al. (1997).

We conducted six intensive behavior watches of radio-tagged birds (Table 4.2). At the beginning of each behavioral watch, we selected one individual to track from birds within the area recorded by the receiver station (Advanced Telemetry Systems, Inc. Model R4000) at Point Doran. After selecting an individual, we approached to within 100-200 m of the bird using a combination of visual identification and transmitter signal gain. We then observed and documented the bird's behavior (diving, on the water, flying) visually if possible, and/or by the presence and absence of the audible signal, as the signal tone disappeared completely when the bird was underwater.

In addition to intensive foraging behavior watches, we also continuously monitored the presence and movement of radio-tagged Kittlitz's Murrelets for much of the breeding season using three remote data-logging receivers (Advanced Telemetry Systems, Inc. Model R4500S) (Fig. 4.1). We used a 12-volt marine battery, continually recharged by a small solar panel, to power the remote data-logging receivers. The stations continuously scanned for all tag frequencies, spending 12-s searching each individual frequency per cycle. If a tag was detected, receivers remained on the frequency for 10-s.

An individual was considered present if three additional signals were recorded. Bird presence data were compiled by 10-min intervals.

4.3.4 Stable isotope analysis

Isotope ratios were determined for blood and feather samples at the Cornell Stable Isotope Laboratory. Samples were dried, ground and weighed prior to stable carbon and stable nitrogen isotopes analyses. Two standards were used during the analysis to assure quality control: a pure chemical standard to test instrument linearity and responses, and an in-house standard, calibrated to international standards, to test long-term instrument stability (Cornell University Isotope Laboratory). Isotopic ratios are the parts-per-thousand (δ notation) difference in the ratio of the rarer and heavier isotope to the more common, lighter, isotope (i.e. ^{15}N to ^{14}N or ^{13}C to ^{12}C), compared to the isotope ratio observed in international standards, where:

$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000 \quad (4.1)$$

and X is equal to either ^{15}N or ^{13}C and R is equal to the ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$, respectively (Bearhop et al. 2002).

After calculating $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for Kittlitz's Murrelet blood and feather tissue samples, we then corrected these values using fractionation factors to account for the assimilation of prey signatures into Kittlitz's Murrelet tissues. We used fractionation factors of 1.1 and 0, respectively, for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of blood samples, following field experiments of Cassin's Auklets (*Ptychoramphus aleuticus*) and Rhinoceros Auklets (*Cerorhinca monocerata*) (Cherel et al. 2005, Davies 2007). For the secondary feather

clip, we used estimated fractionation factors values of 3.7 for $\delta^{15}\text{N}$ and 1.0 for $\delta^{13}\text{C}$ calculated from experiments with Common Murres (*Uria aalge*) (Becker et al. 2007). Additionally, to account for the influence of lipid content on stable carbon isotope values for prey items where carbon to nitrogen isotope ratios are >3.5 , we used $\delta^{13}\text{C}$ values from samples that either had lipids chemically extracted before isotope analysis or $\delta^{13}\text{C}$ values that were corrected for lipid content post-analysis (Post et al. 2007).

4.3.5 Stable isotope statistical tests and modeling

We used Program R (R Core Development Team 2010) for all statistical analyses. Using the isotope values from Kittlitz's Murrelet samples, we first tested for a difference between tissue types, as well as for a difference between sexes for a given tissue type using a two-sided student's t-test with unequal sample variances. Next, we used the collection of potential prey stable isotope signatures to examine Kittlitz's Murrelet diet using SIAR, a Bayesian isotope mixing model that incorporates the variance in prey source signatures in the model (Parnell et al. 2010). For the best representation of possible prey species, we used only prey samples from PWS, Icy Bay and the northern GOA in our analysis of early breeding season diet, as individuals generally arrive at breeding season habitats during April and May (Day and Nigro 2004, Arimitsu et al. 2011). To analyze post-breeding diet (from 5th secondary feather clip samples), we included all prey samples from PWS, Icy Bay, the GOA, and the Bering Sea. Although individuals appear to leave PWS quickly following the breeding season (authors, pers. obs.), suggesting the birds do not typically undergo the fall molt while still in PWS, occasionally adult Kittlitz's Murrelets are observed in winter plumage in PWS during

July and August (authors, unpubl. data). Therefore, we included prey samples from all regions in the post-breeding diet analysis.

After calculating the relative proportion of each individual prey source in Kittlitz's Murrelet tissue samples, we combined individual prey sources into broader ecological groups by summing among sources within a group (A. Parnell, pers. comm.). We used general life history characteristics of potential prey species to assign ecological groups. For example, northern lampfish were assigned to the mesopelagic category, and walleye pollock to the demersal category, even though both species may occur in near surface waters in glacial fjords (Abookire et al. 2002, Arimitsu 2009). We then calculated the average and 95% credible intervals for each ecological group. For the analysis of early breeding season blood samples, we categorized individual prey sources into four groups: zooplankton, near-surface pelagic fish, mesopelagic fish and demersal fish (Table 4.1). For the post-breeding feather analysis, we additionally qualified each group as including Bering Sea samples vs. samples from the GOA region (Table 4.1). Because of the potential spatial and temporal variability in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ among prey species (e.g., Williams et al. 2008, Kline 2010), our probable prey groups and model results represent a general assessment of Kittlitz's Murrelet diet, rather than a description of specific prey taxa. We elected to use data from as many likely Kittlitz's Murrelet prey species as possible in our analysis, as we currently know virtually nothing about Kittlitz's Murrelet diet.

4.3.6 At-sea foraging behavior data analysis

We calculated the duration of foraging bouts, loafing bouts, and average dive and rest times for each individual bird observed for the behavioral watches. We classified foraging bouts

as the elapsed time during which >3 dives were recorded, with a final rest time lasting >3 min (Jodice and Collopy 1999). Loaf times were classified as the elapsed time between foraging bouts. Dive times were measured using a combination of the elapsed time the radio signal was lost and visual observations, when possible. We calculated foraging, loafing, average (\pm SD) dive and rest times per bout per individual, using only complete bouts. A bout was considered complete when we observed a subsequent behavior (i.e. loafing after foraging). We then calculated average foraging bout, loafing bout, dive, and rest times for each individual by averaging across all bouts. Finally, we averaged the individual values to calculate overall average and 95% confidence intervals for foraging bout, loafing bout, dive, and rest times.

4.4 Results

4.4.1 Stable isotope statistical analyses

We analyzed 33 blood samples (14 males and 19 females) and 37 feather samples (16 males, 18 females, 3 undetermined) for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. There were no differences between sexes for either blood tissue samples ($\delta^{15}\text{N}$: $p = 0.24$, $\delta^{13}\text{C}$: $p = 0.16$) or feather tissue samples ($\delta^{15}\text{N}$: $p = 0.37$, $\delta^{13}\text{C}$: $p = 0.56$). Among birds, the average \pm SD for $\delta^{15}\text{N}$ was 12.13 ± 0.67 and $\delta^{13}\text{C}$ was -19.20 ± 0.69 for blood samples. Feather clips averaged 14.32 ± 0.38 for $\delta^{15}\text{N}$ and -19.95 ± 0.20 for $\delta^{13}\text{C}$. There were differences between the early breeding diet (blood samples) and post-breeding diet (feather clips) for both $\delta^{15}\text{N}$ ($p = < 2.2 \times 10^{-16}$) and $\delta^{13}\text{C}$ ($p = 7.47 \times 10^{-07}$) (Fig. 4.2).

Our Bayesian isotope mixing model results indicated that Kittlitz's Murrelets diet during the early breeding season was partitioned into 36% (95% credible interval = 29–45%) zooplankton, 22% (12–36%) near-surface pelagic fish, 22% (9–41%) mesopelagic fish, and 19% (4–29%) demersal fish (all GOA prey; Fig. 4.3). During the post-breeding season, Kittlitz's Murrelets diet was partitioned into 39% (32–44%) Bering Sea demersal fish, 26% (22–32%) Bering Sea near-surface pelagic fish, 10% (8–14%) GOA mesopelagic fish, 9% (6–15%)

Bering Sea zooplankton, 9% (5 – 15%) GOA near-surface pelagic fish, 9% (7 – 12%) Bering Sea mesopelagic fish, 4% (2 – 8%) GOA zooplankton, and 0% (0 – 1%) GOA demersal fish (Fig. 4.4).

4.4.2 At-sea foraging behavior

We observed five individuals (4 males and 1 female) during six tracking efforts, for a total of 34 hr (per track mean = 5.6 ± 2.4 hr), representing 12 complete foraging bouts and eight complete loafing bouts (Table 4.2). Average foraging bouts lasted 25.1 min (95% CI = 14.2 – 36.1 min), and average loafing bouts lasted 120.3 min (95% CI = 41.8 – 199.0 min) (Table 4.3). Within a foraging bout, individuals averaged 34 dives per bout (95% CI = 20 – 49 dives per bout). Dive times within a given foraging bout were relatively short, lasting 22 s on average (95% CI = 18.5 – 25.4 s), while rest times among individuals showed greater variation with an average time of 27.3 s (95% CI = 13.4 – 41.3 s) (Table 4.3). We did not find a relationship between foraging behavior and tide height (Fig. 4.5).

Remote logging stations monitored the presence of nine of the 12-tagged individuals over 45 days between 21 May and 14 July. For the other three birds, one individual was regularly recorded between 21 May to 30 June; it was apparently killed by a Peregrine Falcon (*Falco peregrines*) soon after 30 June. Another individual was recorded several times by aerial surveys at a potential nest site, and we suspect that this bird regularly used a fjord south of our study area. The signal for a third bird was recorded only a few times before we found its tag at a Bald Eagle (*Haliaeetus leucocephalus*) perch soon after tagging. The nine individuals regularly recorded throughout the monitoring period were present within the Harriman Fjord/Barry Arm region roughly 40% of the time (95% CI = 27.4 – 53.6%). For the five individuals manually tracked, all were present over 20% of the time (average = 45, 95% CI = 38 – 53%) within the Harriman Fjord/Barry Arm. Most of the birds left Harriman Fjord/Barry Arm at night, presumably to spend

the dark hours in more open waters. On average, radio-tagged Kittlitz's Murrelets were recorded at the furthest south remote logging station (either Barry Arm or Esther Island) on 52% (95% CI = 40.4 – 64.8%) of the 45 observation nights. The five Kittlitz's Murrelets manually tracked spent nearly all their time during daylight hours close to the moraines near Point Doran.

4.5 Discussion

4.5.1 Breeding season diet and foraging behavior

During the early breeding season, Kittlitz's Murrelets foraged on a combination of zooplankton and fish. The high proportion of zooplankton prey (36%) and fairly low proportions of high-lipid prey species, such as near-surface pelagic fish species (22%) (e.g., Pacific herring, Pacific sand lance and capelin) and mesopelagic fish species (22%) (e.g., northern lampfish) (van Pelt et al. 1997, Iverson et al. 2002, Logerwell and Schaufler 2005, Whitman 2010, Vollenweider et al. 2011) was unexpected. These results suggest that Kittlitz's Murrelets are generalist foragers during the early breeding season, possibly a result of prey availability. We would expect that individuals would target the most nutritious prey, unless the availability of these preferred species was so low that eating a higher volume of less nutritious species yielded higher levels of net energy gain (Stephens and Krebs 1986). This generalist foraging strategy may be sufficient to meet the relatively lower energetic requirements during this time period in comparison to the more energetically intensive chick-rearing period (Ricklefs 1983, Simons and Whittow 1984, Roby 1991), though females may have higher nutritional demands than males during egg production (Ricklefs 1974). Further, when self-feeding during the early breeding period, adults do not face the same travel constraints that they face during incubation and chick rearing. The birds therefore may not need to target exclusively high quality prey (e.g., near-surface pelagic and mesopelagic fish); rather they maintain body reserves by eating a combination of zooplankton and fish.

Our observations of Kittlitz's Murrelets foraging in rapid bouts interrupted by long loafing periods may be related to ephemeral prey concentrations. When prey items are solitary, a predator can allocate dive times with longer rest periods between dives without decreasing foraging success (Clowater and Burger 1994). However, individuals foraging on schooling prey need to forage more rapidly; while the likelihood of prey capture is high once a school of prey is located and the likelihood of finding the school again after a long rest period is low (Ydenberg and Clark 1989). The long loafing periods between Kittlitz's Murrelets foraging bouts could also reflect the need for a prolonged period of digestion. Indeed, invertebrate species, which contributed high relative proportions of early breeding diets, take a longer time to digest than fish (Jackson et al. 1987, Davis et al. 1998). Additionally, the observed average rest time of 27.3 s for Kittlitz's Murrelets is over twice the average rest time length for Marbled Murrelets (10 – 12 s, Peery et al. 2009, Pontius and Kirchoff 2009) that typically consume a larger proportion of fish than Kittlitz's Murrelets (Day et al. 1999). Cairns (1987) suggested that a combination of rapid foraging bouts, extended loafing periods and fairly consistent dive times and foraging patterns similar to our observations of Kittlitz's Murrelets are all likely indications that birds were working near their full energetic capacity. The tidal cycle may also play a role in the timing of foraging bouts. Although we did not observe a clear pattern between foraging behavior and tidal height, Kittlitz's Murrelet abundance in fjords is influenced by tide height and time of day (Allyn et al., unpublished data); many seabird species are known to concentrate foraging efforts where tidal currents aggregate prey (e.g., Decker and Hunt 1996, Irons 1998).

Our study suggests that Kittlitz's Murrelets may be a species with a relatively inflexible time budget during the breeding season. Any additional increase in energetic demands caused by disturbances to foraging activity, a reduction in prey abundance, or prey quality could decrease productivity (Suryan et al. 2000, Litzow and Piatt 2003). Notably, Kittlitz's Murrelet daytime foraging habitat in PWS appears to overlap strongly with areas of high tourist vessel traffic

(Murphy et al. 1999). During two foraging watches, we observed foraging birds cease diving when our vessels passed close by, possibly the result of disturbance or scattering of the prey. Disruption of foraging bouts may not only limit an individual's ability to eat and obtain food for young (Speckman et al. 2004), but could also increase flight behavior and therefore the amount of energy expended (Agness et al. 2008), resulting in considerable net energy losses. Persistent disruptions of foraging birds could reduce body condition with detrimental effects on survival and productivity (Monaghan et al. 1989, 1992, Chastel et al. 1995).

Most PWS researchers noted that Kittlitz's Murrelets disappear from hotspot areas during the late afternoon and evening hours; for this reason, surveys generally are conducted between 0700 and 1600 hrs (Kuletz et al. 2003, 2011). However, where they were going when they leave these daytime areas was a mystery. Our observations using remote logging stations recorded most of our tagged birds leaving the fjord during the nighttime, with some traveling ~20 km south of Harriman Fjord to areas near the Esther Island tracking station. Further, the nearshore waters of Esther Island are a major salmon gillnetting area during the summer months, which may pose a threat to Kittlitz's Murrelets.

4.5.2 Post-breeding diet

Following the breeding season, Kittlitz's Murrelet diet is apparently more specialized than the generalist diet of the early breeding season, as evidenced by the considerably lower isotope variance observed in early breeding tissue samples ($\delta^{15}\text{N}$ SD = 0.38, $\delta^{13}\text{C}$ SD = 0.20) compared to post-breeding samples ($\delta^{15}\text{N}$ SD = 0.67, $\delta^{13}\text{C}$ SD = 0.69). Additionally, a large proportion of Kittlitz's Murrelets post-breeding diet was attributed to Bering Sea demersal fish and Bering Sea near-surface pelagic fish (e.g., Walleye pollock, Arctic cod, Pacific herring, Capelin). These results indicate that either Kittlitz's Murrelets become more specialized in prey preference during the post-breeding season, or that they are responding to a decrease in available

prey diversity, possibly the result of reduced foraging ability during the flightless molt period. It seems unlikely that Kittlitz's Murrelets shift their diet to demersal fish species over near-surface pelagic or mesopelagic fish species, considering demersal fish species are generally lower in nutritional quality (Anthony et al. 2000). This suggests that Bering Sea demersal fish species are the prey most readily available to flightless birds at molting locations.

Our results suggest that Kittlitz's Murrelets that summer in PWS probably winter in the Bering Sea region. Since the value of $\delta^{13}\text{C}$ varies depending on the photosynthetic source, and generally does not change considerably with changes in trophic levels (Kelly 2000), the significant difference in Kittlitz's Murrelet early breeding and post-breeding $\delta^{13}\text{C}$ is likely a response to a large shift in Kittlitz's Murrelet foraging locations. Recent studies of satellite-tagged Kittlitz's Murrelets document that some PWS birds travel to the Bering Sea very soon after the breeding season (J. F. Piatt, unpubl. data). Furthermore, recent pelagic surveys reported Kittlitz's Murrelets in the open water polynyas of the northern Bering Sea during late winter and early spring (K. J. Kuletz, unpubl. data). Together, these results strongly indicate that Kittlitz's Murrelets embark on long migration flights from breeding habitats to over-wintering habitats, a costly venture for a species with high wing-loading (Pennycuik 1987). The efficiency with which individuals are able to locate and consume quality prey during these trips could strongly influence their over-winter survival as well as their reproductive success the following year (Aldrich and Raveling 1983, Weimerskirch et al. 1993, Chastel et al. 1995).

The pre-basic molt, which Kittlitz's Murrelets undergo following the breeding season, may be the most significant foraging constraint individuals face throughout the year. During this extended period of flightlessness, individuals must locate and capture prey through swimming alone. Although our results suggest that most sampled individuals left PWS to molt, occasional observations of winter plumaged adults in PWS during July and August suggest that some individuals, possibly non-breeding birds who are not actively provisioning chicks in July and

August, do choose to molt in PWS. Regardless of the eventual molting location, Kittlitz's Murrelets may be exceptionally susceptible to shifts in the distribution or abundance of predictable, quality prey resources during this flightless period.

4.6 Acknowledgements

The National Fish and Wildlife Foundation and the US Fish and Wildlife Service provided funding for this project. We thank Peter Crommett for his dedicated fieldwork throughout the summer, and Aaron Poe (USFS) and Joel Schmutz (USGS) for telemetry data collection support and tracking equipment. Michelle Kissling (USFWS) and Nick Hatch (Oregon State University) provided extensive guidance on capture and sampling techniques, and Tom Bloxton Jr. (USFS) provided on-site capture training. We also thank Dr. Andrew Parnell for his helpful insight on stable isotope analysis methods, and Mayumi Arimitsu for her helpful comments and review of an earlier draft of this manuscript.

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Table 4.1. Species, ecological group, region group, sample location, sample source, and average and standard deviations (SD) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ prey sample isotope signatures used in investigating Kittlitz's Murrelet early breeding season and post-breeding season diet. GOA = Gulf of Alaska, PWS = Prince William Sound.

Species	Prey Group	Region	Location and Source	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$
<i>Neocalanus cristatus</i>	Zooplankton	GOA	PWS, Kline 2010	8.7	1.9	-19.5	1.4
<i>Euphausiidae</i> sp.	Zooplankton	GOA	GOA, Hobson et al. 1994	11.1	0.84	-18.6	2.04
<i>Hyperiid</i> sp.	Zooplankton	GOA	Icy Bay, N. Hatch (unpubl. data)	10.45	0.72	-20.39	0.19
<i>Mysidae</i> sp.	Zooplankton	GOA	Icy Bay, N. Hatch (unpubl. data)	10.57	0.1	-15.38	0.07
Pacific sandlance (larval) (<i>Ammodytes hexapterus</i>)	Near-surface pelagic fish	GOA	Icy Bay, N. Hatch (unpubl. data)	9.92	0.12	-21.43	0.15
Pacific sandlance (year 1)	Near-surface pelagic fish	GOA	Icy Bay, N. Hatch (unpubl. data)	12.33	0.54	-18.71	0.57
Pacific herring (<i>Clupea pallasii</i>)	Near-surface pelagic fish	GOA	PWS, A. Allyn (unpubl. data)	12.75	0.62	-18.36	0.29
Capelin (<i>Mallotus villosus</i>)	Near-surface pelagic fish	GOA	PWS, A. Allyn (unpubl. data)	12.7	0.44	-18.71	0.49

Eulachon (<i>Thaleichthys pacificus</i>)	Near-surface pelagic fish	GOA	PWS, A. Allyn (unpubl. data)	12.7	0.95	-18.56	0.93
Surf smelt (<i>Hypomesus pretiosus</i>)	Near-surface pelagic fish	GOA	Icy Bay, N. Hatch (unpubl. data)	13.11	0.77	-18.83	0.46
Northern lampfish (<i>Stenobranchius leucopsarus</i>)	Mesopelagic fish	GOA	PWS, Kline 2010	13.1	0.9	-19.2	0.8
Northern lampfish	Mesopelagic fish	GOA	GOA, Kline 2010	10.7	1.7	-21.4	0.6
Pallid Eelpout (<i>Lycodapus mandibularis</i>)	Demersal fish	GOA	PWS, Kline 2010	14.7	1	-18.6	0.4
<i>Calanoida</i> copepod sp.	Zooplankton	Bering Sea	Bering Sea, Cui 2009	8.2	2.3	-18.9	4
<i>Ampeliscidae</i> sp.	Zooplankton	Bering Sea	Bering Sea, Cui 2009	12.3	0	-18.9	0
<i>Hyperiid</i> sp.	Zooplankton	Bering Sea	Bering Sea, Cui 2009	10.1	1.2	-18.8	1.3
<i>Lysianassidae</i> sp.	Zooplankton	Bering Sea	Bering Sea, Cui 2009	12.3	1	-14.4	1.6
<i>Melitidae</i> sp.	Zooplankton	Bering Sea	Bering Sea, Cui 2009	10.5	0.8	-17.1	0.2

Capelin	Near-surface pelagic fish	Bering Sea	Bering Sea, Cui 2009	15	0.9	-19.75	0.8
Pacific herring	Near-surface pelagic fish	Bering Sea	Bering Sea, Cui 2009	15.7	0.9	-20	1.9
Walleye Pollock (<i>Theragra chalcogramma</i>)	Demersal fish	Bering Sea	Bering Sea, Cui 2009	15.4	0.7	-21.3	0.4
Arctic Cod (<i>Boreogadus saida</i>)	Demersal fish	Bering Sea	Bering Sea, Cui 2009	16.3	0.7	-20	0.6

Table 4.2. Date, duration and number of foraging bouts and rest periods observed during intensive focal watches of radio-tagged Kittlitz's Murrelets in northwestern Prince William Sound, Alaska, 2009.

Date	Individual	Sex	Duration		Foraging bouts	Loafing bouts
			Time	Total hours		
18 June	A	Male	1018-1700	7	2	1
30 May	B1	Male	1044-2031	10	3	3
28 May	C	Male	0700-1105	4	2	2
27 May	D	Male	1425-1814	4	2	1
24 May	E	Female	1132-1644	5	1	0
23 May	B2	Male	1153-1533	4	2	1

Table 4.3. Summary of manually tacking behavior watches, including loaf duration, foraging bout durations, number of dives, and average dive and rest times \pm standard deviation for each bird and averaged (\pm 95%CI) for each behavior. Inc. = Incomplete records, where the signal was lost before we were able to determine the end of activity A and beginning of activity B.

Bird ID	Loaf Duration (decimal min)	Foraging bout duration		Average dive time (s) (\pm SD)	Average rest time (s) (\pm SD)
		(decimal min)	# of dives		
A	268.3	5.3	7	25 \pm 16	24 \pm 20
		Inc.	16	27 \pm 9	64 \pm 146
B1	12.5	40.3	37	30 \pm 6	16 \pm 12
	36.5	10.2	5	15 \pm 6	133 \pm 120
	224.8	26.4	47	21 \pm 5	13 \pm 4
	Inc.				
C	124.3	40.2	62	29 \pm 10	10 \pm 3
	71.6	Inc.	9	13 \pm 11	22 \pm 8

D	118.2	8.2	18	12 ±3	16 ±17
		23.6	52	18 ±3	10 ±6
E	Inc.	44.6	66	27 ±4	14 ±15
B2	26.2	27.9	43	25 ±3	15 ±12
		10.3	14	16 ±9	31 ±20
AVERAGE	120.3	25.1	34	22.0	27.3
95% CI	41.8-199.0	14.2-36.1	20-49	18.5-25.4	13.4-41.3

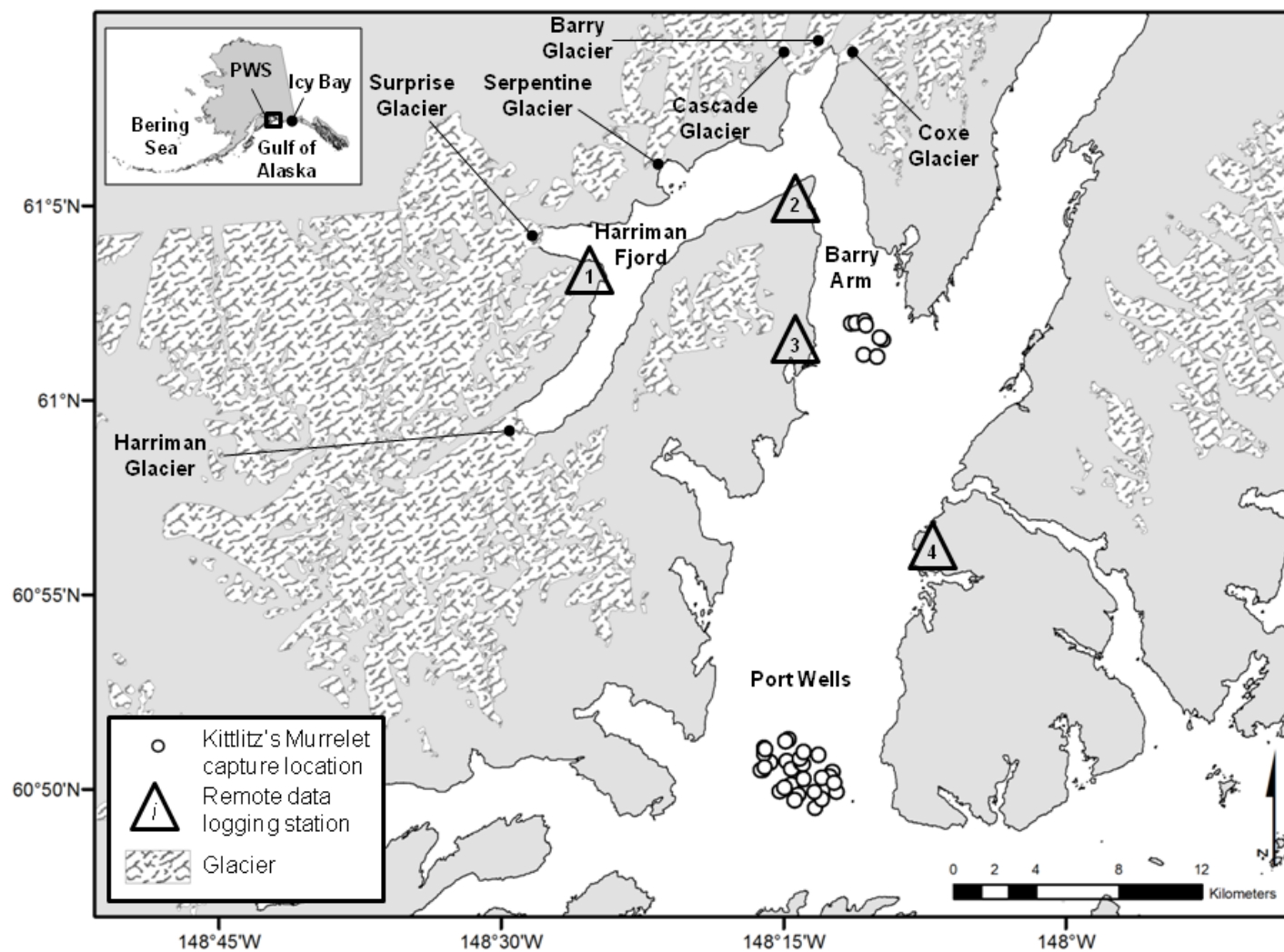


Figure 4.1. Northwestern Prince William Sound study area, Kittlitz's Murrelet capture locations, and remote data-logging stations, 2009. Remote data-logging station 1 and station 2 were deployed throughout the entire monitoring period (21 May – 14 July). On 30 June station 3 was relocated to the station 4 location.

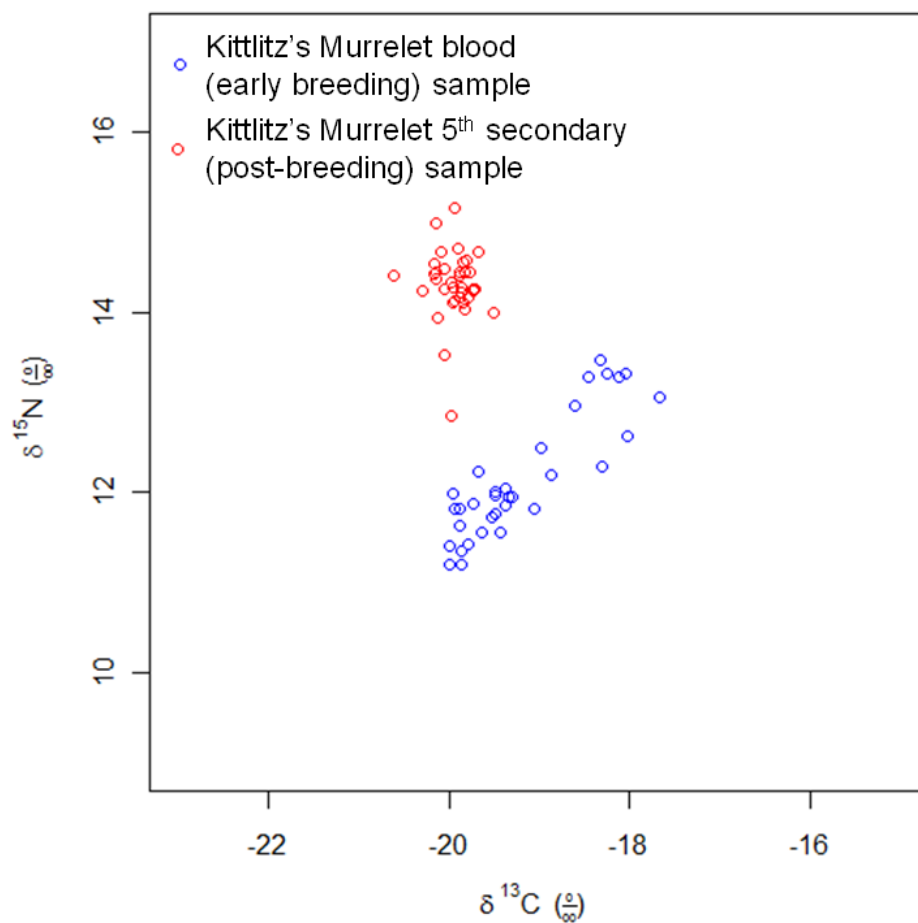


Figure 4.2. Stable isotope $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plots of Kittlitz's Murrelet blood (early breeding) and 5th secondary (post-breeding) samples collected for individuals captured in northwestern Prince William Sound, Alaska, 2009.

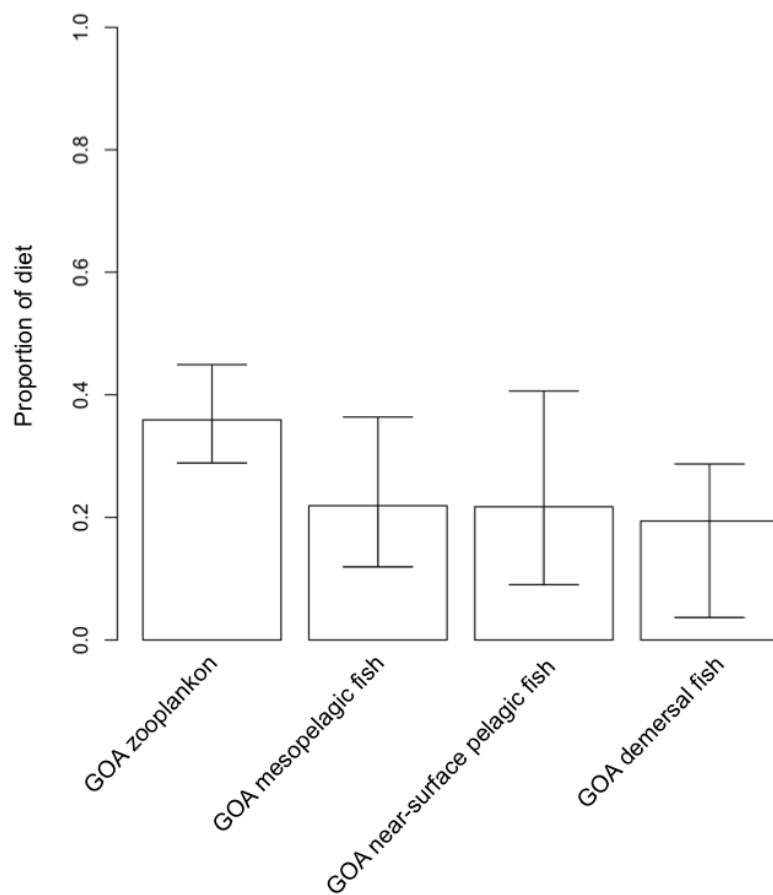


Figure 4.3. Average diet composition and 95% credible intervals of early breeding season Kittlitz's Murrelet blood samples for Gulf of Alaska (GOA) zooplankton, GOA mesopelagic fish, GOA near-surface pelagic fish, and GOA demersal fish.

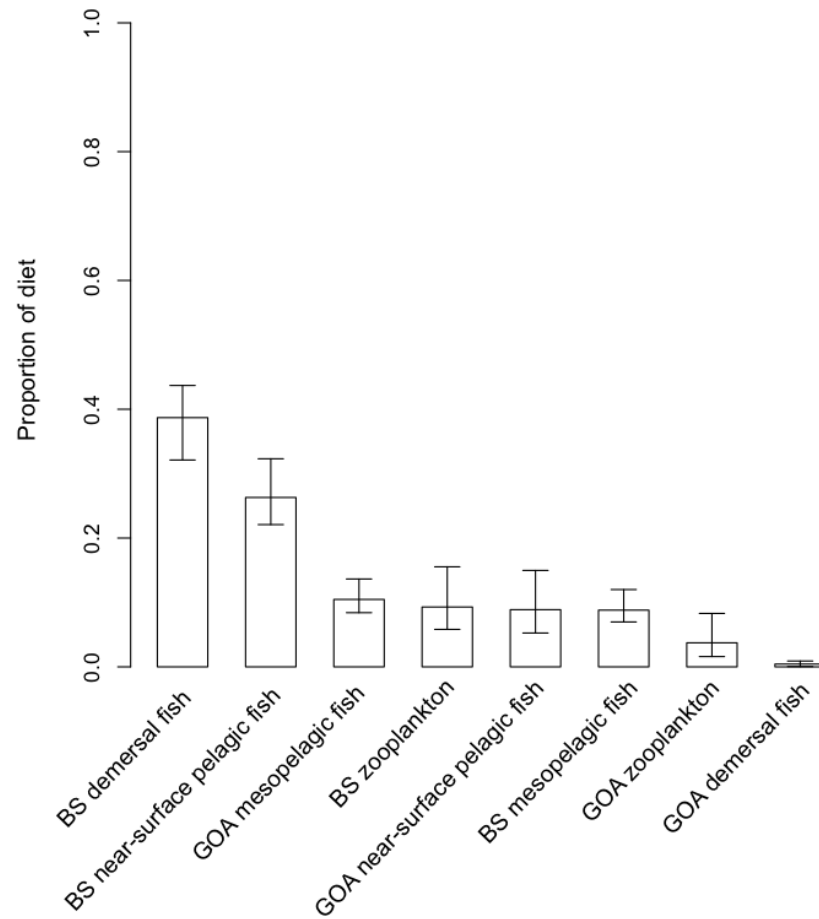


Figure 4.4. Average diet composition and 95% credible intervals of post-breeding season Kittlitz's Murrelet feather samples for Bering Sea (BS) demersal fish, BS near-surface pelagic fish, Gulf of Alaska (GOA) mesopelagic fish, BS mesopelagic fish, BS zooplankton fish, GOA near-surface pelagic fish, GOA zooplankton, and GOA demersal fish.

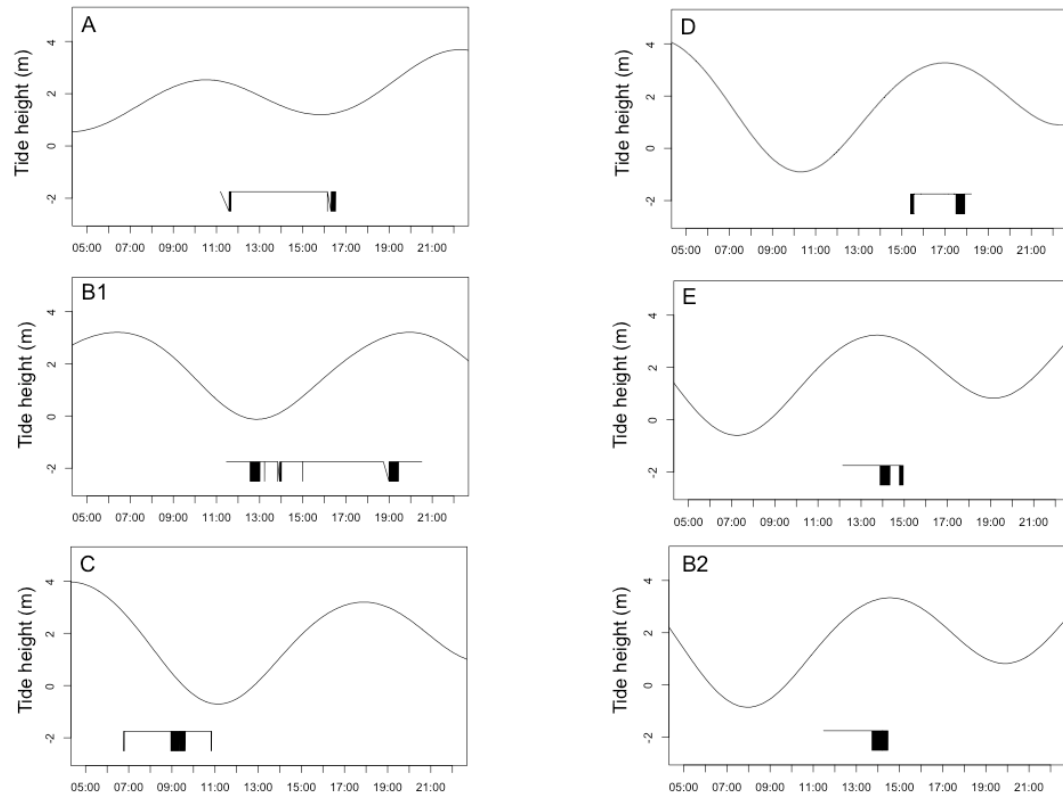


Figure 4.5. Kittlitz's Murrelet foraging behavior during boat-based tracking of radio-tagged individuals depicting loafing (represented by a horizontal line) and diving behaviors (represented by a vertical line) by time of day, plotted with daily tide height curves.

CHAPTER 5

CONCLUSIONS

Populations of Kittlitz's Murrelets have undergone widespread declines in recent decades throughout many core population regions in Alaska, including PWS (Kuletz et al. 2003, 2011). In response to these declines, the Kittlitz's Murrelet is currently listed as a candidate for the United States Endangered Species List (USFWS 2011). However, the reasons behind these declines remain elusive, largely the result of Kittlitz's Murrelets solitary and cryptic nesting behavior, which makes collecting basic ecological data on survival and productivity virtually impossible. Given our lack of understanding of the factors driving the declines, it is understandably difficult to craft effective management strategies.

Our study of Kittlitz's Murrelet population size, habitats and diet in PWS began to fill in some of these gaps in our understanding of this population. First, despite decreasing during the late 1980s through to the early 2000s, the population appears to have stabilized since between 2001 and 2009, and may have even increased slightly. Secondly, our habitat use model, based on data collected from a broader range than any previous PWS habitat work, indicated Kittlitz's Murrelets use habitats that are shallower, closer to glaciers, and closer to shore and further from moraines than the average available habitat. Our more intensive habitat work investigating water column properties suggest that temperature-depth profiles also influenced Kittlitz's Murrelet habitat use in two PWS fjords that regularly host sizable numbers of Kittlitz's Murrelets. Third, our stable isotope work showed that during the pre-breeding season, Kittlitz's Murrelets were generalist foragers, consuming a variety of zooplankton and fish species. However, during the post-breeding season, individuals appeared to forage exclusively on demersal and near-surface pelagic fish species, likely from the Bering Sea. This post-breeding specialization may be a

consequence of the flightless period Murrelets go through during the autumn molt. Additionally, demersal and near-surface pelagic fish may constitute the majority of available prey in the Bering Sea during this time period. Intensive watches of radio-tagged Kittlitz's Murrelets showed individuals forage in rapid bouts separated by long loafing periods, suggesting that individuals may be responding to ephemeral prey concentrations and possibly working near their maximum energetic capacity. In combination, this new information both fills necessary data gaps concerning the species general ecology, and also provides vital information that may be useful in guiding conservation and management actions.

Effective strategies for preserving Kittlitz's Murrelet populations will need to improve survival and/or productivity rates in threatened populations. For Kittlitz's Murrelets, habitat degradation, shifts in quality prey availability, natural and human caused mortality, and human caused disturbance all are factors likely to affect population survival and productivity rates. Changing climate and environmental conditions may contribute substantially to habitat degradation for this glacially-associated species through the wasting of tidewater glaciers. Such changes in the ecosystem undoubtedly influence the spatial distribution of quality prey. Human activity in the region, such as commercial fishing, may further compound these prey distribution effects. Considering the global scale of climate change, state and federal management decisions are unlikely to mitigate these problems in the near future. Instead, management actions will likely focus on decreasing vessel disturbance, which may reduce foraging success and increase energetic costs. Reducing human-caused mortality in the form of bycatch should also be a goal of any management policy.

The degree to which Kittlitz's Murrelets are threatened by human activities is a function of the spatial overlap between Kittlitz's Murrelet distributions and human use patterns. Our research across 17 fjords and bays supports previous findings; Kittlitz's Murrelets in PWS use

glacial fjord habitats during the daytime. However, because these fjords are also common ecotourism and commercial fishing areas, managers will need to take action to effectively protect Kittlitz's Murrelets while simultaneously minimizing the cost to the vital fishing and tourism industries in these areas. Compounding the issue is the new revelation that at night, Kittlitz's Murrelets travel out of the fjords and into areas where they are rarely seen in the daytime; areas that can be subject to intensive gillnetting activity. Because the presence of Kittlitz's Murrelets in these areas is highly dependent on time of day, a minimal-impact management strategy might be to close fishing for a few hours in the night when birds are most likely to be present.

The conservation of important habitat is generally deemed an cost-effective short-term strategy when population control mechanisms are unknown, given the pervasive threat of habitat loss and degradation, and this approach does not require extensive long-term datasets to estimate population vital rates, which are economically and logistically costly to collect. This conservation strategy hinges upon our ability to develop cost effective, expedient, and accurate methods for delineating important habitat areas. Our habitat use model provides an efficient way to delineate small patches within glacial fjords, with high accuracy, which could be targeted for potential conservation actions, including, for example, setting vessel speed limit. Further research, possibly using location tags, may also provide opportunities for delineating conservation areas targeting Kittlitz's Murrelet nighttime habitat use. In combination, both of these strategies would help reduce any potential threats posed by the overlap of Kittlitz's Murrelets and human use while we continue to evaluate the mechanisms controlling the population dynamics of this rare and elusive species.

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